The Paleozoic

The Paleozoic Era of the Phanerozoic Eon: 542 to 251 million years ago

The Paleozoic (also spelt "Palaeozoic") era lasted from about 540 to 250 million years ago, and is divided into six periods The 320-odd million years of the Paleozoic era saw many important events, including the development of most invertebrate groups, life's conquest of land, the evolution of fish, reptiles, insects, and vascular plants, the formation of the supercontinent of Pangea, and no less than two distinct ice ages. The earth rotated faster than it does today so days were shorter, and the nearer moon meant stronger tides. - MAK

The Paleozoic - 1

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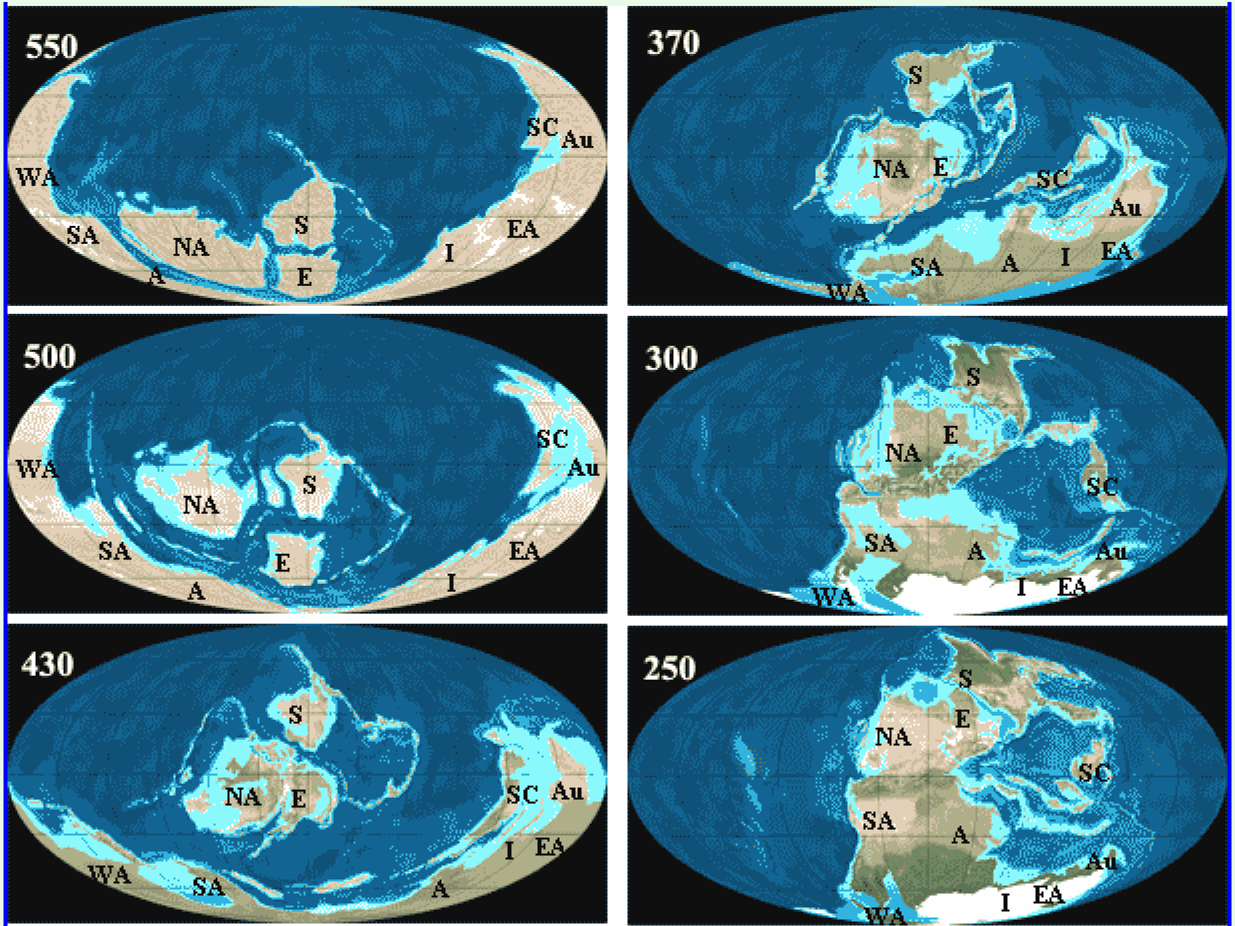
MAK

Paleozoic Geography

Since the continental cratons all move with respect to each other, we need to pick an East-West point of reference to keep things straight. Paleozoic



A = Africa
Au = Australia
E = Europe (Baltica)
EA = E. Antarctica
I = India
NA = N. America (Laurentia)
S = Siberia
SA = S. America
SC = South China
WA = W Antarctica

Arrangement of major continents at intervals (in Mya) during the Paleozoic. Adapted from Blakey. Apparant changes in size are due to distortion inherent in the map projection.

paleocartographers have somehow fallen into the habit of placing this reference longitude slightly east of Greenland. For most of the Paleozoic, Greenland remained close to the equator and, after Baltica sutured to Laurentia (North America plus Greenland) during the Silurian, this longitude came to correspond quite closely to the longitude of the future Greenwich, England, which defines the present conventional 0° longitude line. We will adopt this convention, although it is important to understand that it's just a convention. We have no absolute measures of East-West continental drift, and must be content with noting movements relative to some arbitrary geographical point.

The early Paleozoic saw many of the continents clustered around the equator, with Gondwana (representing the bulk of old Rodinia) slowly drifting south across the South poles, and Siberia, Laurentia (North America plus Greenland) and Baltica converging in the tropics. There was a large ocean between Laurentia and Eastern Gondwanaland.

It seems that Gondwanaland underwent a large clockwise rotation around an axis close to Australia during the Early Paleozoic. Laurentia underwent a large eastward movement, as well as a northward drift.

Baltica joined with Laurentia during the Silurian, drifting from a moderate southern hemisphere position in Cambro-Ordovician time to an equatorial position in Silurian-Devonian time. The combined continent is sometimes referred to as Euramerica, Laurasia, or Laurussia. Siberia, and possibly the Kazakhstan terranes, drifted across the equator to the northeast. All the East and Southeast Asian terranes, as well as the microcontinents which later formed Mexico, the east coast of North America, and southern Europe, were still part of the north coast (India-Australia margin) of Gondwana during the Early Palaeozoic.

During the middle and late Paleozoic (Devonian to Permian), about a third of the Gondwanan mass was torn into small pieces and moved rapidly to equatorial regions. Most of these blocks were assembled by a series of plate collisions into the supercontinent of Euramerica by the Devonian, which by addition of further landmasses became Laurasia by the late Carboniferous. Most of western Gondwana (South America and Africa), then rotated clockwise and moved northward to collide with Laurasia. By Permian time, Siberia and the Kazakhstan terranes were sutured to Euramerica (Laurussia) and the Chinese blocks started accreting to them. The result was the supercontinent Pangaea. MAK, revised ATW050810.

Paleozoic Stratigraphy

eon	era	period	when began myrs ago ICS	duration myrs ICS
Phanerozoic	Mesozoic	Triassic	251	51
	Paleozoic	Permian	299	48
		Carboniferous	359	60
		Devonian	416	57
		Silurian	444	28
		Ordovician	488	44
		Cambrian	542	54
Proterozoic	Neoproterozoic	Ediacaran ("Vendian")	630	88

MAK

Paleozoic Climate

The Cambrian climate was probably moderate at first, becoming warmer over the course of the period, as the second-greatest sustained sea level rise in the Phanerozoic got under way. However, as if to offset this trend, Gondwana moved south with considerable speed, so that, in Ordovician time, Most of West Gondwana (Africa and South America) lay directly over the South Pole. The Early Paleozoic climate was also strongly zonal, with the result that the "climate", in an abstract sense became warmer, but the living space of most organisms of the time -- the continental shelf marine environment -- became steadily colder. However, Baltica (Northern Europe and Russia) and Laurentia (eastern North America and Greenland) remained in the tropical zone, while China and Australia lay in waters which were at least temperate. The Early Paleozoic ended, rather abruptly, with the short, but apparently severe, Late Ordovician Ice Age. This cold spell caused the second-greatest mass extinction of Phanerozoic time.

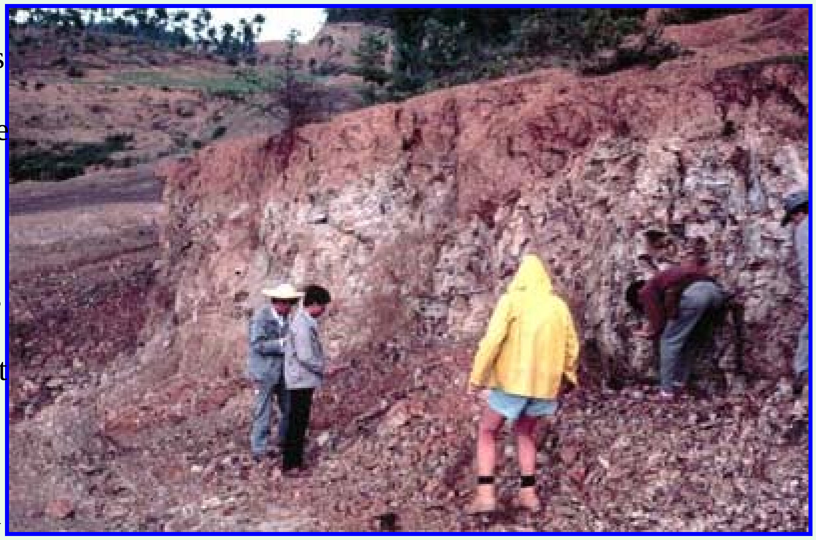
The Middle Paleozoic was a time of considerable stability. Sea levels had dropped coincident with the Ice Age, but slowly recovered over the course of the Silurian and Devonian. The slow merger of Baltica and Laurentia, and the northward movement of bits and pieces of Gondwana created numerous new regions of relatively warm, shallow sea floor. As plants took hold on the continental margins, oxygen levels increased and carbon dioxide dropped, although much less dramatically. The north-south temperature gradient also seems to have moderated, or metazoan life simply became hardier, or both. At any event, the far southern continental margins of Antarctica and West Gondwana became increasingly less barren. The Devonian ended with a series of turnover pulses which killed off much of Middle Paleozoic vertebrate life, without noticeably reducing species diversity overall.

The Late Paleozoic was a time which has left us a good many unanswered questions. The Mississippian Epoch began with a spike in atmospheric oxygen, while carbon dioxide plummeted to unheard-of lows. This destabilized the climate and led to one, and perhaps two, ice ages during the Carboniferous. These were far more severe than the brief Late Ordovician Ice; but, this time, the effects on world biota were inconsequential. By the Cisuralian, both oxygen and carbon dioxide had recovered to more normal levels. On the other hand, the assembly of Pangea created huge arid inland areas subject to temperature extremes. The Lopingian is associated with falling sea levels, increased carbon dioxide and general climatic deterioration, culminating in the devastation of the end-Permian extinction.

Image: Devonian sea floor scene from the **OTS Heavy Oil Science Center**.

Paleozoic Sites

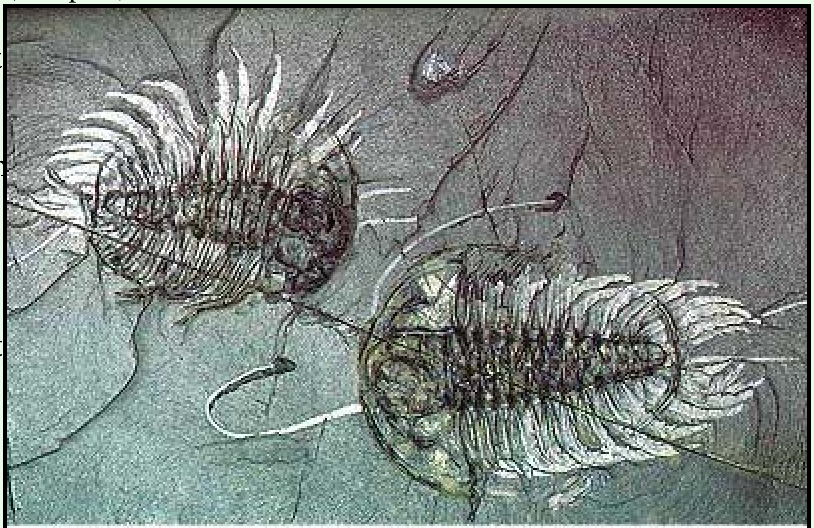
As one might expect from such a vast interval of time, there are a great many Paleozoic sites to choose from. Rather than attempt the impossible task of describing the scars left by 300 My of geological time, we thought we would briefly summarize the ten Paleozoic sites which, in our judgment, had left the greatest mark on paleontology. That, at least, is what we thought. As it turned out, after going through the agonizing job of paring down the list, we found that we could not get much below twelve or fifteen sites. Rather than make some kind of difficult, rational choice, we have simply hacked off the Permian and about half the Carboniferous, as well as randomly discarding some of the many Devonian sites. So you will not see anything from Isheevo or the Karoo, the red beds of Texas, Mazon Creek, Bear Gulch or even Canowindra. Some of these sites are covered in detail elsewhere on this site (which is, of course, one of the ten indispensible sites of Holocene time). Accordingly, without wasting a single electron or pixel more on vain regrets:



1) Chengjiang: Terreneuvian of South China. This site is discussed at Chenjiang. The English spellings are somewhat variable, "Chenjiang" being another popular variant. The correct spelling seems to be 澄江. It might be better to referred to as the Maotianshan Shale. This is less accurate (it is more properly the Qiongzhusi Formation), but seems least likely to be misspelled by ignorant foreigners, such as ourselves. The Chengjiang fossils are dated at 525-520 Mya, or perhaps a bit younger, corresponding most nearly to the Botomian Age in our system **[1]**. Outcrops of the Qiongzhusi occur in scattered locations south of Kunming in eastern Yunnan Province, Chengjiang County, near the towns of Chengjiang and Ercai. Additional sites have now been opened further south. Of all the sites mentioned here, Chengjiang is geologically the oldest and historically the youngest. The fossil potential of the region was discovered by Dr. Hou Xianguang in 1984. Many of the fossils have been recovered – and many lost forever -- in connection with phosphate mines in the area. The incredible soft-tissue preservation of the fossils here seems to have resulted from rapid burial, complete sediment anoxia, and replacement of organic remains with pyrite or phosphates -- nothing magical, except the absolutely unreasonable number of such sites, of varying ages, in Yunnan Province.

The faunal list from Chengjiang is a virtually complete census of the major metazoan taxa of the time, and includes our personal favorite of all early chordates, *Haikouella*. There seems to be little selectivity. There are now Chengjinag fossil images all over the web. However, many of the Chengjiang organisms remain undescribed, simply for lack of competent describers, and new specimens are being discovered at an extraordinary rate.

2) The Burgess Shale: Middle Cambrian of Canada. The Burgess Shale is slightly younger than Chengjiang. The Shale is located near the town of Field, in southeastern British Columbia, high in the Canadian Rockies. The closest major town is Banff, about 90 km to the east. The site was discovered by Charles Walcott of the Smithsonian Institution in 1909, and the Walcott Quarry is named after him. The deposits are deepwater, benthic sediments, but the fauna probably represent a reef community swept off the reef and buried in an anoxic bottom by a mudslide. The Burgess is actually far less spectacular than Chengjiang, but it attained great fame (ironically, just at the time that Chengjiang was starting to produce large quantities of fossils) due in part to Jay Gould's book, **Wonderful Life**.



Olenoides serratus. Two beautifully preserved trilobites from the Burgess Shale, showing legs and antennae. Length of block shown here c. 20 cm.

The Burgess Shale's influence on paleontology has been, in part, due to the fact that Gould chose this book to set out some of his most interesting and controversial ideas about evolution, and in a manner readable by almost everyone. Gould argued that the end results of evolution were essentially random because the process was chaotic **[2]**. Thus even the tiniest change in Proterozoic conditions might have resulted in an entirely different modern fauna. His proof was the diversity of phyla in the Shale, hinting at an enormous initial diversity in the Cambrian Explosion which was quickly pruned away, largely by happenstance. As it has turned out, Gould was certainly wrong about the Burgess Shale. Chengjiang -- and closer examination of the Burgess fauna -- have shown that Walcott was more correct than Gould. The great majority of Burgess animals can now be assigned with confidence to well-known phyla. However, his ideas about evolution may well be correct, if the pruning process actually occurred in the lower Early Cambrian or even before metazoans became morphologically recognizable.

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Paleozoic Sites, cont'd

3) Much Wenlock: The Silurian Much Wenlock exposures are located near the town of the same name in Shropshire, England, on the Welsh Borderlands. This was the edge of a vast Middle Silurian reef, now exposed as a limestone ridge, the Wenlock Edge -- just one more set of wooded Shropshire hills in a now absurdly civilized setting.

The Ordovician and Silurian have left us few famous sites. We chose the Much Wenlock site because it is one of the best of a bad lot. At that, it's not really so bad. Well over 600 species of invertebrates have been found there. These include crinoids, corals, brachiopods, trilobites, algae and bryozoans. Much Wenlock may be less famous than the two Cambrian sites because there are few vertebrates. No one expects vertebrates in the Cambrian, but the early Silurian is part of the dark age of hidden vertebrate diversity, and its rather frustrating that so few are to be found at Much Wenlock. A more serious problem with the Much Wenlock exposures is that many are in limestone quarries (such as the Farley Quarry in the image) which are long abandoned and now filled with water.

As a paleontological site, Much Wenlock is about as old as geology itself. It is part of the region from which the Silurian System was first described by Murchison in the late 1830's. The astute reader may already have deduced as much from the fact that the "Middle Silurian" is officially named the Wenlock. From northwest to southeast, virtually the entire Silurian system is laid out in a series of gently sloping ridges. The impact of Much Wenlock on paleontology lies partly in that early discovery and partly in the early opportunity it gave geologists to put together a the components of a fairly complete Paleozoic ecosystem.

4) Saaremaa Island: If its Silurian vertebrates you're after, this is the better choice. Saaremaa Island is located just off the coast of Estonia, in the Baltic Sea. The entire island rests on Wenlock to Ludlow reef limestones which were buried under Baltic marine sediments until early Holocene times. The topography is quite low, so exposures are relatively rare except on a few bluffs referred to locally (and rather optimistically) as "cliffs." During most of the last century, it was the private preserve of a few scientists from Moscow, Talinn, and occasionally Stockholm.

Saaremaa is not particularly well known, although it has yeilded any number of often beautifully preserved jawless fishes, in addition to eurypterids and other shelled invertebrates. Perhaps we over-rate its importance; but perhaps not. Our belief is that more systematic exploration of Saaremaa and some even more obscure sites in Poland, has the potential to transform our understanding of vertebrate evolution.

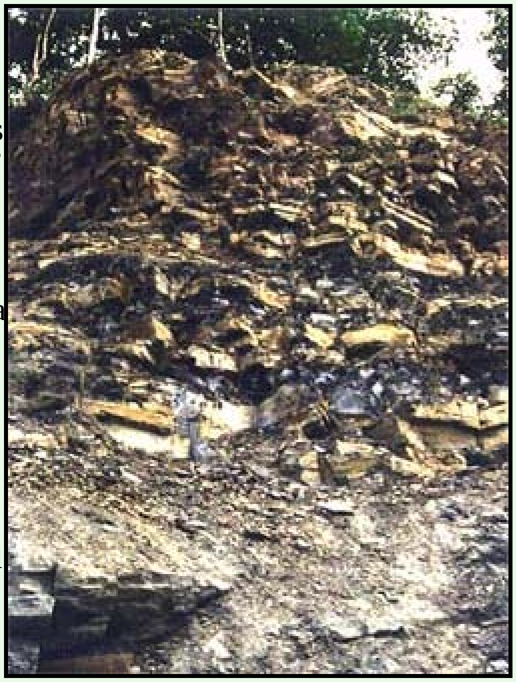
5) Spitsbergen: This location is sometimes spoken of in the same breath as Saaremaa. Spitsbergen is actually a bit large to be referred to as a "site." It is the largest member of the Svalbard, a large arctic archipelago located well north of Norway. It is unreasonably cold and beautiful and is inhabited entirely by scientists and polar bears. At least that is the impression one gets. Undoubtedly this is an exaggeration, and many of the polar bears will turn out to be Norwegian scientists -- or vice versa. The base of the sedimentary sequence at Spitsbergen is the Red Bay Formation, largely of Ludlow and Pridoli age. The exposures continue right into the Cenozoic in various localities. For paleontologists, however, most of the interest is in the Red Bay and Early Devonian Wood Bay groups, both exposed in the relatively glacier-free center of the island.

These are immense exposures. Collection collections are difficult, and vertebrate fossils are seldom common in any Paleozoic site. However, with whole mountains of Ludlow and Early Devonian sediments available, remarkable finds have been made. Fossil prospecting has been going on here since approximately the 1880's. Some well-known results of that work are the three-dimensional fossils of Osteostracan headshields -- with the internal cartilage so perfectly preserved that Janvier, Wängsjö, and others have been able to trace, in detail, the branching paths of the cranial nerves in fishes dead for 400 My.

6) The Rhynie Chert: this is one of the earliest more-or-less terrestrial sites known. Rhynie is located in Aberdeenshire, Scotland, about 50 km west of Aberdeen. It was first found and its plant fossils studied by Robert Kidston and William Lang in 1917. The Rhynie Chert represents a swampy peat bog from the Early Devonian with the peculiar addition of mineral springs. The plant tissues were preserved by silicate diagenesis, in which the plant tissues were replaced by silicates from the springs almost immediately after burial. The preservation is practically miracuous in some cases, extending almost to subcellular organelles. In addition to plants, there

are Fungi and numerous arthropods, mostly crustaceans and spiders, with a few early insects.

The Rhynie Chert has allowed us to study early terrestrial plants in considerable detail. However, more than this, it shows how the entire community was structured. The community in question was, no doubt, aberrant for that time or any other. Nevertheless, we see every component from predatory spiders down to fungal saprophytes. No other site from a comparable time period gives us such a detailed look at an entire terrestrial community.



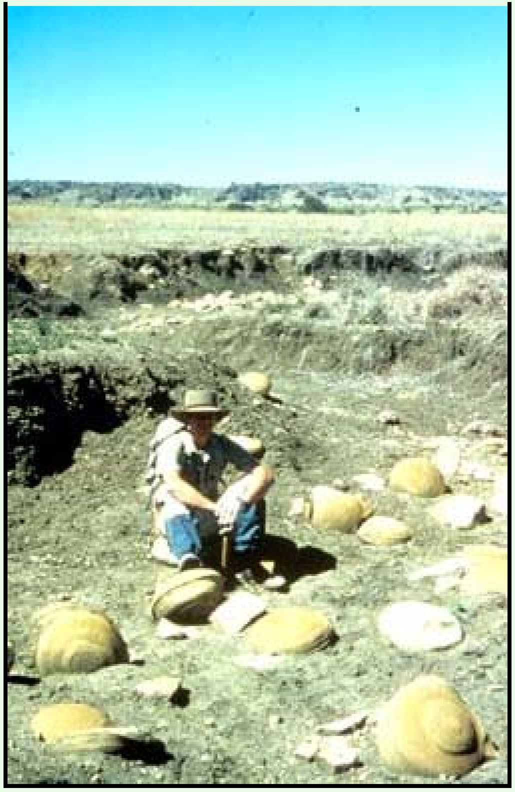
7) Escuminac or Miguasha: The Canadian towns of Miguasha and Escuminac **[3]** are located on the Gaspé Penninsula, on the Quebec side of the rather optimistically named Baie-des-Chaleurs, across from the north coast of New Brunswick. This exceedingly famous site is referred to by both names because the best exposure of the Escuminac Formation is at Escuminac Cliff which, naturally enough, is located in Miguasha. This exposure is of Frasnian (Late Devonian) age. It was first discovered in 1842 by Dr. Abraham Gesner (the man who invented kerosene). It was then forgotten until rediscovered in 1879 by Robert W. Ells of the Canadian Geological Survey. Miguasha represents a near-shore environment, parts of which are choked with ferns and terrestrial plants. The best fossils are found in calcareous nodules which probably allowed very fine and undistorted replacement of bone by carbonates.

It is now a UNESCO World Heritage site, so designated because "[t]he area is of paramount importance in having the greatest number and best preserved fossil specimens found anywhere in the world of the lobe-finned fishes that gave rise to the first four-legged, air-breathing terrestrial vertebrates -- the tetrapodes [sic]." Close enough, we suppose, for government work.

In some ways, Miguasha is a monument to one man, Erik Jarvik. Over the course of about 50 years, Jarvik published a series of papers on painstakingly prepared specimens of *Eusthenopteron*, "Le Prince de Miguasha." These were ground down, in tiny increments, with each new surface studied in minute detail, until the entire three-dimensional structure of the fish's cranial and axial skeleton was understood. This work was complemented by two massive papers in 1970 by Mahala Andrews and T. Stanley Westoll, who said what there was to say about the appendicular skeleton. Andrews & Westoll (1970), (1970a). At the time, and perhaps until just the last few years, this was the most complete reconstruction of a paleozoic vertebrate ever completed.

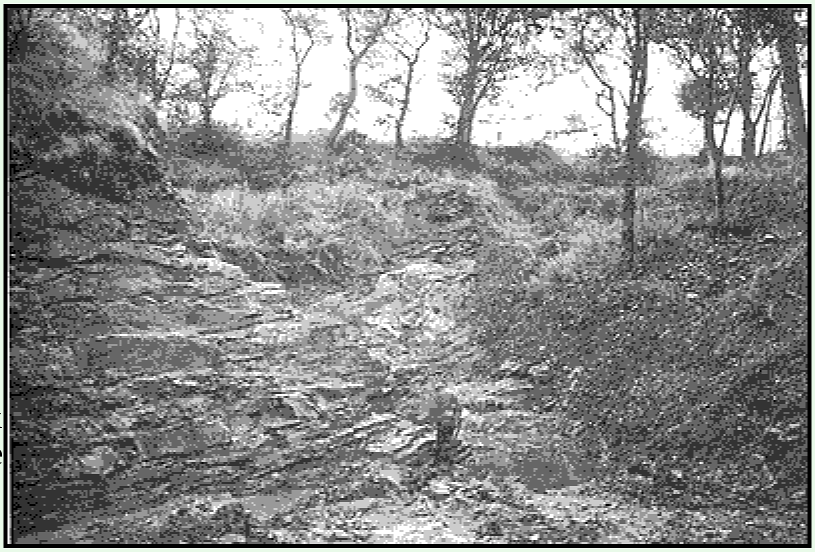
It is impossible to overstate the importance of this kind of detailed restoration. In the Late Nineteenth Century, Huxley was instrumental in changing paleontology from a branch of geology which happened to study once-living rocks, to an evolution-centered science. Huxley had lots of help, but he set the standard. In the same way, Jarvik's work on *Eusthenopteron* helped set the standard which is now allowing paleontology to move from the evolution of structure to the evolution of *function*. This requires knowing, not just where the bones are and what general shape they had, but exactly how they articulated, where and how large the attached muscle masses were, and how the moving parts were ennervated to form a living, moving organism.

8) Gogo Reef: The Gogo reef looks, from the air, like a reef that someone left out in the Australian desert. Since Australians tend to be a rather



straightforward folk, that's exactly what it is. The Gogo Reef is in the northwestern part of the State of Western Australia in what is vaguely referred to as the Kimberly District. It is conveniently located near nothing. There is no road. It is, in fact, so far from any town with a name recognizeable by non-Australians that it would be pointless to get any more specific. Evenif we recognized the name, we would inevitably pronounce it wrong, and the Australians would laugh at us -- not a pretty sound. The Gogo is truly in the middle of nowhere. The image shows some typical limestone concretions from the Gogo, presided over by a typical Australian paleontologist, John Long. He's probably laughing at us anyway.

The whole business is very straightforward and Australian. During the Frasnian, the Gogo Reef was in the water, where it belonged. Things died. Being dead, they fell off the reef and ended up on anoxic bottoms. Tough luck. On the bottom, the chemistry and temperature got them *very slowly* covered with precipitating limestone. There's no soft tissue preservation, mind you, but no crushing, either. The fossils are completely three-dimensional and cemented into limestone nodules. The Australians pick up the nodules, tap them briskly, and -- pop! -- there's your fish, eurypterid, or whatever. They then take the thing home and reverse the natural process by*very slowly* dissolving the limestone with dilute acetic acid. Then they turn on the light, open a beer, and *very slowly* begin to describe the fish, eurypterid, or whatever. Later, sometimes decades later, they turn off the light, kick the empties out of the way, and publish -- long after the rest of us have developed ulcers and bald spots from waiting -- or have ended up on our own anoxic bottoms.



9) East Kirkton: East Kirkton Quarry is located in the town of Bathgate, just about dead in the middle of the legendary (for fossils) Scottish Midland Valley. According to Clack (2002), from whence our image comes, Bathgate is a suburb of Edinburgh. However, it may just as easily be called a suburb of Glasgow. Undoubtedly the Edinburgh cachet adds a few percent to sale prices in the housing development next door to the quarry. In the 1830's and 40's, when the quarry was active, it yeilded some interesting Carboniferous plants and eurypterids, but nothing startling. When the quarry closed, the place was forgotten until (as Clack relates) Stan Wood found tetrapods there in 1984. The quarry was then re-opened and literally dozens of tetrapods came rolling out: *Balanerpeton* (a temnospondyl), *Sivanerpeton* and *Eldeceeon* (basal anthracosaurs), all in multiple copies, and one spectacular proto-amniote, *Westlothiana*.

Not only were these finds interesting in their own right, but they helped to fill in "Romer's Gap," the temporal and phylogenetic gap between rather fishy Late Devonian forms and the amniotes of the Pennsylvanian. East Kirkton is Late Viséan age, so its in the right time frame. Its a big Gap, and we've a very long way to go, but East Kirkton a good start. Incidently, The small figure in the pit is Dr. Clack herself, who is here caught *in flagrantes relictos* (loosely, "among a bunch of amazing fossils").

10) Joggins: The seaside cliffs of Joggins, Nova Scotia are another Canadian UNESCO World Heritage site. This is the famous place where *Dendrerpeton* was stumped in the Pennsylvanian. The Joggins fossils are probably of Bashkirian Age. Their exact placement in time is still somewhat controversial. The site probably represents a coastal swamp thickly covered with large, tree-sized lycopsids. These large lycopsids were not as

structurally sound as today's angiosperms. Their trunks seem to have broken frequently. The central column of lycopsids is soft and rots out much faster than the outer trunk. Normal decay thus left hollow stumps, which became either homes or traps for small animals living in the swamp. Their remains can be found in fossilized stumps, frequently in an excellent state of preservation. The basal temnospondyl, *Dendrerpeton* and several other small vertebrates are among those which have been recovered because of this unique mode of preservation.

One of the reasons that Joggins is so significant is that it has preserved what are normally the rarest fossils -- the small vertebrates; and it has preserved them often in fully-articulated form. This is a valuable check on our ideas about the evolution of vertebrates as we approach the huge diversity of forms in the Permian and beyond.

On Beyond Joggins: some day we hope to return and fill in the Karoo locales, Isheevo, Ocher, and other Permian sites. However, Permian tetrapod sites are really the products of a whole different taphonomic style. Forthe moment, this will have to do.

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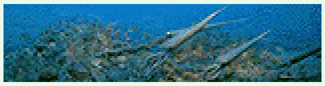
The Paleozoic - 3

Paleozoic Life

Life changed so much during the Paleozoic - from seaweed to forests, from proto-chordates to mammal-like synapsids - that it is difficult to summarize. Although Paleozoic means "ancient life" many of the organisms that lived during the later Paleozoic were much closer to those of today than many of the life-forms of the early Paleozoic. Basically, at the risk of generalization, we might say that the earlier Paleozoic was dominated by invertebrates, while the land remained barren. The middle Paleozoic saw the rise of strange armoured fish and the first land plants and insects. While the later Paleozoic was distinguished by great forests of mostly spore-bearing trees, inhabited by a rich assortment of arthropods, tetrapods and reptiles on land; and by diverse invertebrates in the sea.



Cambrian eco-systems were much simpler and less diversified than anything of today, and hence unstable and prone to easy mass-extinction. Moreover, it is possible to distinguish an earlier Tommotian type fauna (Terreneuvian) from a Middle Cambrian to Early Ordovician fauna.

The initial flowering of metazoans during the Early Cambrian (the "Cambrian Explosion") spread animal life throughout the seas. The typical Furongian marine community was dominated by trilobites, "inarticulate" brachiopods, and eocrinoids. However, the basic pattern for Ordovician and Middle Paleozoic marine communities was established in the great Early Ordovician radiation of marine metazoans. "The Palaeozoic evolutionary fauna originated and diversified during an early Ordovician radiation event. Many of the adaptations high-lighted in the Palaeozoic marine benthos are associated with soft substrates. Articulate brachiopods, stenolaemate bryozoans, stalked echinoderms (crinoids and blastoids), corals, ostracodes diversified together with graptolites within the water column. Most plankton groups may have been recruited from the benthos while events within the plankton ecosystem were shadowed by changes in benthic systems (Rigby and Milsom. 1996). The vigorous early Ordovician radiation set the agenda for much of the Palaeozoic; the majority of adaptations in the invertebrate groups had already been tried and tested by the end of the Ordovician." Benchley & Harper (1998).

Following the large end-Cambrian and end-early Ordovician extinctions, a new evolutionary fauna originated and diversified during the Ordovician radiation event. This constituted a Palaeozoic marine benthos associated with soft substrates. Articulate brachiopods, stenolaemate bryozoans, stalked echinoderms (crinoids and blastoids), corals, ostracodes all diversified. Higher up in the water column, the plankton and nekton included graptolites and conodonts, cephalopods, and later fish and medusa (scyphozoa). This vigorous early Ordovician radiation set the agenda for much of the Palaeozoic; and most adaptations by the various invertebrate groups had already been tried and tested by the end of the Ordovician. By the Middle to Late Paleozoic marine ecosystems may not have been too unlike those of today. Ecosystems and energy and nutrient flow on land was much more inefficient, until the rise of reptilian herbivores at the very end of the era (late Permian).

Perhaps the most intelligent creatures to inhabit the earth over this long span of time were the cephalopods, the most intelligent and sentient of all the invertebrates. Cephalopods were extraordinarily diverse in Paleozoic seas, and were the dominant life-form until the rise of carnivorous fish during the Devonian (mid-Paleozoic). At the very end of the Paleozoic the Therapsida evolved larger brains than their contemporaries, and paved the way for mammalian intelligence during the Mesozoic and Cenozoic.

The Paleozoic witnessed a number of crises in the history of life, including an early Cambrian, a terminal Cambrian, an Ordovician one, a late Devonian one. The era was brought to an end by the terminal Permian extinction, the greatest catastrophe in the history of higher life on Earth (although far milder than the Early Proterozoic Oxygen crisis). There is still disagreement over whether it was caused simply by terrestrial phenomena like loss of geographic isolation and falling sea-levels, or whether (as I feel likely) these factors were aided by an extraterrestrial impact of some kind (similar to the one that saw off the dinosaurs at the end of the Mesozoic). MAK, ATW050819.

Paleozoic Benthos

The Burgess Shale fauna -
A Cambrian seafloor in what is now Field, British Columbia.
The jellyfish-like blue organisms at far left are *Eldonia*.
The yellowish upside-down animals are *Canadaspis*, the brown sponge clusters *Vauxia*

note: the following passage is from Patrick J. Benchley and by D. A. T. Harper, *Palaeoecology* (I have included a note in brackets].

"During the first 10 million years of the Cambrian Period the Tommotian fauna was replaced by a more diverse biota of larger metazoans participating in more complex communities. The Cambrian fauna was dominated by low-level suspension feeders such as the nonarticulate brachiopods and eocrinoids together with monoplacophoran and hyolith mollusks. Two parazoan groups developed colonial strategies: the archaeocyathans and possibly the sponges. Colonies tend to develop iteratively with new iterative units or modules derived by continuous growth from existing units. The colonial or iterative body plan thus contrasts with the unitary or solitary life mode of most organisms. A number of groups show clear trends towards a greater integration of individuals within the colony and in some cases a differentiation of functions across the colony.

Trilobites were the most abundant members of the Cambrian benthos; in many assemblages over 90% of the animals were trilobites [note - although trilobites represent the most common fossil that doesn't mean they were the most common animal. Trilobites had a hard carapace, molted frequently, hence they left a disproportionately numerous record of themselves compared to other creatures living at the same time]. Cambrian communities were loosely organized and considerable experimentation and morphological flexibility were features of many troops (Hughes, 1994). Cambrian *Lagerstätten* such as the Burgess Shale contain a wide range of apparently morphologically disparate organisms."

note: the following passage is from pp. 128-137 of the same text

The low-level Paleozoic benthos was dominated by fixed suspension feeders, mainly the brachiopods supported by the bryozoans and microcarnivores such as the rugose and tabulate corals. Mollusks were generally rare, although some bivalve-dominated associations occur throughout the Paleozoic and may have inhabited specialized habitats. The spongelike stromatoporoids were responsible for carbonate buildups, particularly during the mid-Paleozoic, when they developed a range of growth modes including columnar, dendroid, encrusting and hemispherical forms (Kershaw, 1990).

By the mid-Ordovician, two major groups of anthozoans, the rugose and tabulate corals, were firmly established as microphages, although neither ever built substantial reef structures, lacking many of the adaptations, such as a basal plate, that helped the scleractinians to develop as the dominant reef-builders of the Modern fauna.

Paleozoic corals also advanced the development of colonial or compound life strategies. Tabulate corals developed only colonial forms, many fine-tuned for life on a soft substrate; the location, orientation. spacing and development of offsets in the corallites have been developed in a tool-kit of adaptations for different substrates.

Brachiopods dominated a range of nearshore to shelf-edge environments, suited to a variety of substrates at a range of water depths in marine conditions. The group was the principal epifauna of the Paleozoic. Certain basic aspects of the brachiopod morphology, such as the presence or absence of a pedicle, had a major control on the brachiopod life strategy. More subtle features of the animal, for example the size, shell shape and ornament, also had clear adaptive significance.

Crinoids, together with brachiopods, dominated the Paleozoic sessile benthos. The crinoids developed a range of articulatory structures allowing the stem considerable flexibility. Although most crinoids are and were fixed, rheophile organisms, orientating their crowns into the current when feeding, some such as the Recent comatulid *Antedon* are mobile or attached by small roots or cirri, whereas the Jurassic *Saccocoma* may have been either epiplanktonic or part of the free-living benthos

Evolution, initially, in the crinoids of discoidal holdfasts permitted attachment to hard substrates; however, the development of more versatile root-like holdfasts allowed the group to target soft, muddy substrates commonly located in more offshore environments (Sprinkle and Guensburg, 1995). This transition between these two types of attachment structures may have driven a large-scale diversification of the group and its expansion into deeper-water environments during the early Paleozoic.

Bryozoan diversified during the Ordovician radiation, building larger and more complex colony types. Initially colonies were low with few zooids; multi-story complexes were developed to occupy available space and evolve efficient feeding strategies.

Only a shallow infauna was well developed in the Paleozoic fauna, although there were exceptions; it included bivalves, scaphopods, trilobites and crustaceans occupying depths of up to about 100 mm. Nevertheless, by the early Carboniferous, trace fossil data suggests that depths of up to one meter of sediment were penetrated by bivalves. Bivalves first appeared during the early Cambrian as part of a shallow infauna. Throughout the Phanerozoic the group has demonstrated a remarkable spectrum of adaptive morphologies for life above, at and within the sediment-water interface. Aspects of the Paleozoic bivalve fauna heralded the intense infaunal radiation of the group during the Mesozoic Marine Revolution, when the group became much more dominant.

Tiered profiles evolved during the Paleozoic (Ausich and Bottjer, 1982). The intermediate-level benthos (50-200 mm) was dominated by sponges, corals, giant bivalves, giant brachiopods, stalked echinoderms and fixed dendroid graptolites. High-level sessile benthos (200-500 mm) contained mainly crinoids and blastoids. The stalked echinoderms concentrated on improving the efficiency of their feeding techniques with the development of more elaborate calices.

Trilobites continued to dominate the mobile benthos, although bivalves, gastropods and echinoids locally moved across and through the sediment. Cephalopod mollusks such as the orthoconic nautiloids patrolled the benthos, in a role as the main macrophagous predator.

The following sequence of bottom-living biotas, defined according to major extinctions, adaptive radiations, and community reorganizations, is suggested for this period by Arthur Boucot (Phanerozoic Extinctions: How similar are they to each other?", *Lecture Notes in Earth Sciences 30*, Springer-Verlag Berlin Heidelberg 1990). Note that these do not always follow or equate with the Terrestrial or Freshwater succession:

- Early Ordovician
- Mid to Late Ordovician
- Llandovery (Early Silurian)
- Siluro-Devonian
- Famennian (Late Devonian)
- Carboniferous-Permian

MAK

Reef Systems

Even using an elastic and generous definition of "reef," the only reef systems prior to the Paleozoic were stromatolites: large, and sometimes very large, mounds formed by successive layers of bacterial biofilms. The first "real" reefs were formed in the last half of the Terreneuvian by Archaeocyatha, rather poorly known lacy, sponge-like creatures which became

extinct in the Middle Cambrian. From that point until the Middle Ordovician, the only reefs were "mud mounds," somewhat variable mixtures of stromatolite, sponges, and a sort of filamentous red algae that bound everything together. In the Middle Ordovician, encrusting Bryozoa became part of the mix.

However, large biogenic reefs remained rare until the Late Ordovician, when an entirely new type of reef began to be constructed based on a framework of tabulate and colonial rugose corals together with stromatoporoid sponges. The hallmarks of Paleozoic marine ecosystems are probably these tabulate or rugose coral reef. These corals initially (Early and Middle Ordovician) were part of a reef-building guild which included bryozoans and stromatoporoids, among others. These mixed communities supported a community largely made up of suspension feeders. The corals probably came into their own in connection with the Late Ordovician glacial period. They were then associated with more complex ecosystems which supported a mobile fauna including eurypterids, ammonoids, and fishes with jaws.

These "tabulate-strome" reefs remained the dominant form of reef for almost 100 My, until the Late Devonian. A really good source of information on tabulate strome communities is the Milwaukee Public Museum's **Virtual Silurian Reef** site, from which we have borrowed the adjacent image.

In the Late Devonian, many groups turned over rapidly. We hesitate to label it a mass extinction, since species-level diversity seems to have suffered little, if at all. Nevertheless, the Carboniferous fauna was markedly different from the Late Devonian in many respects. Reef builders were no exception. The pattern may then have been reset, paradoxically, by a series of events associated with the spread of terrestrial plants and culminating in the Mississippian Ice Age. Stanley (2002) (abstract). What happened then is unclear. The nature of marine ecosystems during the Pennsylvanian and Permian seems to be unsettled, and may have differed considerably from place to place. Brachiopods were certainly an important component, as were stalked crinoids. In general, it seems likely that sessile filter feeders were again dominant as in Ordovician times

In addition to whatever factors caused the Late Devonian turnover, the world's ocean chemistry crossed the critical barrier between calcite and aragonite seas. Calcium carbonate can take either of two crystal forms: calcite or aragonite. When magnesium levels are high, aragonite is favored. That is, seawater concentrations of magnesium must have increased to the point that calcium carbonate precipitating from sea water took the form of aragonite rather than calcite. This was bad news for corals which had evolved to use calcite as a basic part of their body plan. Both tabulate and rugose corals were hard hit. Stromatoporoid sponges almost disappeared. Although both coral groups recovered somewhat in the Pennsylvanian, they gradually gave way to more modest reefs constructed by new sponge groups, bryozoans and calcareous algae. Both rugose and tabulate corals became completely extinct at the end of the Permian. *See, generally*, Stanley (1998).

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Pelagic life

note: the following passage is from Patrick J. Benchley and by D. A. T. Harper, *Palaeoecology*, p.137 (Chapman and Hall)

> Acritarchs, chitinozoans and radiolaria had a dominant place in the microplankton. Graptolites formed a large part of the macroscopic plankton and nekton during the early Paleozoic together with pelagic and planktonic trilobites; whereas orthoconic nautiloids together with conodont

animals were probably major predators above the sediment-water interface to be joined by both jawless and gnathostome fishes. A few species of small, thin-shelled bivalves and brachiopods may have pursued epiplanktonic strategies attached to floating organic material or even volcanic pumice.

The Paleozoic - 3

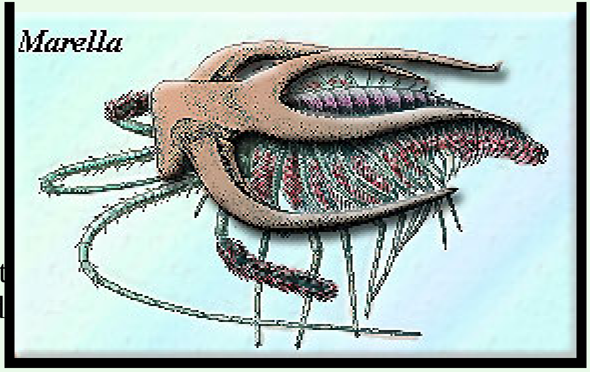
Paleozoic Life (continued)

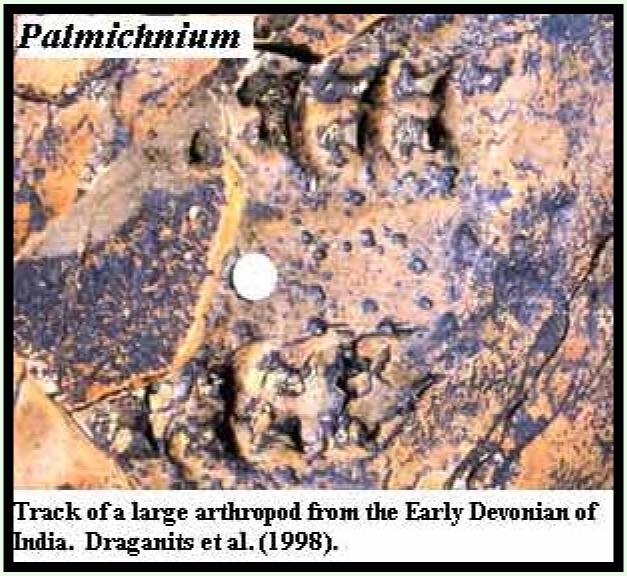
Plants

Plant life on land follows a very different evolutionary pattern - in terms of primary ecosystems - to both land animals and marine life. Whilst the division of the main evolutionary stages of multicellular life into Palaeozoic, Mesozoic, and Cenozoic is described in many popular science books and educational websites, few people are aware that these terms apply to animal life only. Plant life followed a different route, and the paleobotanical time-eras of Palaeophytic, Mesophytic, and Cenophytic are only approximately equivalent. Palaeophytic refers to the primarily spore-bearing (and a few primitive seed-bearing) Paleozoic vascular flora, which appeared in the Middle Ordovician period and die out quite a few millions of years before the end of the Paleozoic (latest early Permian and earlier). In the middle Permian the gymnosperm-dominated Mesophytic flora emerges (although Mesophytic type plants go back to the Carboniferous, just as some Paleophytic plants survive even to this day), and this flourishes right up until the middle and later Cretaceous. MAK010115

Arthropods

Arthropods apparently got off to an early start. By the time of the Burgess Shale in the Middle Cambrian arthropods and their immediate relations were already the most diverse and successful group of animals. The anomalocarids (which were either arthropods or their immediate sister group) were the world's earliest known large predator, with lengths approaching 2 meters. Trilobites are well known from Cambrian Epoch 2 onwards, since their hard carapace fossilizes easily. In addition to trilobites and several other high-level taxa of extinct arthropods, it is almost certain that many of the important arthropod groups of today had already diverged by this time, including the chelicerates, crustaceans, and arachnids. Xiphosurans and some derived crustacean groups are known by the end of the Cambrian. At that time the trilobites experienced several rounds of turnover as the nature of the sea floor environment began to change. Of the miraculous variety of arthropod in the Burgess Shale, only 4 basic designs survived the end of the Cambrian. Of the four, the trilobites were extinguished at the end of the Permian. The remaining three are the insects (Hexapoda), the crustaceans, and the chelicerates.





Track of a large arthropod from the Early Devonian of India. Draganits et al. (1998).

By the Ordovician, some arthropods were at least partially terrestrial. Several different types of arthropod land trackways of this age are now known. Identifiable millipede and arachnids, including scorpion, parts are known from the Silurian. In the seas, eurypterids also got their start during the Ordovician, but only became dominant predators in the Silurian. Xiphosurans (hoseshoe crabs) also flourished in the Silurian. Trilobites were somewhat less common than in the Cambrian, but continued as an important part of the sea bottom fauna.

Terrestrial trace fossils of apparent arthropods are known from the Wenlock (Middle Silurian). Orr *et al*. (2000). Body fossils of identifiable members of the extinct arachnid group Trigonotarbida have been found as early as the Pridoli (latest Silurian). The manner in which arthropods came to land raises some rather deep evolutionary questions. Terrestrial life is so different from life in in water that the barrier to evolution is high. One might reasonably expect that that the transition would occur only rarely and that the first of any large group to accomplish the feat would radiate explosively, preventing any later group which was even remotely similar from getting a foothold on land. So, for example, all land vertebrates descend from a single common ancestor who established itself on land in the Late Devonian. The same can probably be said of land plants, as well as terrestrial worms (Annelida) and mollusks. Arthropods, however, seem to have independently evolved terrestrial forms at least half a dozen times over a relatively long period of time (Pridoli to Mississippian). See, e.g., Klok *et al*. (2002).

Arthropods were well-established on land in the Devonian, and seem to have reached impressive size in some cases. The earliest known Hexapoda -- but not yet insects -- were discovered in Devonian rocks. Terrestrial spiders were present, but trilobites began a serious long-term decline in the seas. The increasing biomass of land plants and higher oxygen levels by the end of the Devonian probably led to the evolution of terrestrial, herbivorous forms by the end of that period, possibly including the first insects.

Insects were certainly present during the Carboniferous, and all of the major groups had diverged by the end of Paleozoic time. Insects with folding wings had evolved by the Pennsylvanian (Late Carboniferous). A few of these, particularly some dragonflies and spiders, reached very large sizes. This may have been due to abnormally high oxygen levels during the Carboniferous. Dudley (1998). However, most Paleozoic insects were as small as insects today. In the seas, the trilobites and eurypterids declined and became extinct at the end of the Permian. Crustaceans became increasingly diverse and successful.

Image: *Palmichnium* image from Draganits *et al*. (1998)

Links: The **SUNY Cortland Geology Department** has a good introduction to the Paleozoic evolution of arthropods.

Trilobites were the most succesful group of arthropods for most of the early Paleozoic. Sam Gon has the most succesful of **trilobite sites** -- and with good reason. Trigonotarbids are introduced at the **UCMP site**.

Terrestrial Ecosystems

The following quotation is from *Terrestrial Ecosystems Through Time* (pp.289-290) and gives an excellent overview of terrestrial Paleozoic biota:

> The Paleozoic was the time during which terrestrial ecosystems were organized and assembled. The plants, invertebrates, and tetrapods can be thought of as three separate subsystems of the larger terrestrial ecosystem. Dominance-diversity patterns, structure, and interactions within these subsystems modernized more or less independently and at different rates throughout most of the Paleozoic. Concomitantly, these three separate subsystems became integrated through trophic interactions and the creation or modification of habitat conditions. This partitioning of ecosystems into "phylogenetic" subunits differs radically from the organization of highly integrated modern systems.
>
> The appearance of structurally and ecomorphically modern plant communities in some parts of the landscape primarily during the Late Devonian and Early Carboniferous included the evolution of life histories, particularly seed habit, that permitted the exploitation of a wide variety of terrestrial environments. The independent evolution of arborescence in nearly all major groups of plants was key to the development of multistratal forests in some habitats at this time. By the Late Carboniferous, complex forest structure and a wide variety of forest profiles and dynamics were clearly in existence across all major land masses.
>
> Global provincialization of vegetation began during the Early Carboniferous and increased more or less continuously until the Permian, when it reached its Paleozoic maximum; this was perhaps the greatest provincialization known prior to the later Tertiary. Such provincialism was made possible by several factors. The physical opportunities increased in diversity and abundance during the Paleozoic as environments changed globally. Because the plants were at the base of the major terrestrial radiation, they evolved increasing tolerances to demanding physical conditions and expanded the extent of the vegetated land surface. This expansion into unoccupied parts of the terrestrial environment was accompanied by an increase in local and regional vegetational heterogeneity, a consequence of local variation in both physical conditions and evolutionary dynamics.
>
> The first animal groups to exploit plant productivity were the arthropods, and then primarily as detritivores. Detritivory was the main entry point of plant primary productivity into animal food webs until the end of the Early Permian. Herbivory, largely by insects, is known from the Early Carboniferous and may have existed in the Devonian. Herbivory expanded rapidly during the Late Carboniferous and was an established part of ecosystem dynamics by the Stephanian or possibly late Westphalian and into the Early Permian. As suggested by the large size of medullosan pollen, insect pollination probably had evolved by the Westphalian. The selective effects of arthropods on plants may be seen in the evolution of sclerotic seed coats and other structural features that would have served to deter post- and pre- dispersal predation. Clear evidence of damage to living foliage does not appear until the later

Westphalian.

Tetrapods were the final element to enter the web of interactions in terrestrial communities. They began, and continued, as carnivores and insectivores through the Carboniferous and Early Permian, situated at the ends of long food chains that were mediated primarily by arthropod detritivory. Although predation on insect herbivores would have shortened some of these pathways and added trophic links to the system, it was not until the expansion of tetrapod herbivory in the late Early Permian that a full integration of the three subsystems was established. The integration had progressed greatly by the Late Permian. However, even by the end of the Paleozoic, the tetrapod component of ecosystems was distinctly different in the sizes, modes of feeding, and range of resources exploited from Mesozoic and younger ecosystems

The following sequence of terrestrial biotas is suggested. These do not always follow or equate with the Marine succession:

Ordovician-Early Silurian (proto-land plants; simple invertebrates)

Siluro-Devonian (early vascular plants, progressing to small trees, many types of arthropods)

Late Devonian - middle Frasnian to late Famennian (proper trees, 30 meters tall, two successive dynasties of tetrapods)

Early Carboniferous (ice age begins, smaller trees; early tetrapods, rhizodont fish top freshwater predators, giant semi-aquatic eurypterids)

Permo-Carboniferous - late Carboniferous to early Permian (ice age continues, mighty tropical coal swamp forests, many tetrapods and early reptiles, winged insects appear, including many giant forms)

Late Permian - drying of climate, extinction of swamp trees and many amphibians and reptiles; therapsids take over, Mesozoic trees and endopterygous insects appear.

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The Paleozoic Era

The Geological Timescale

International Stratigraphic Chart

Period	Epoch	Age	end - began (Mya)
Permian P	Lopingian P3	Changhsingian (or Changxingian) p9	254 - 251
		Wuchiapingian p8	260 - 254
	Guadalupian P2	Capitanian p7	266 - 260
		Wordian p6	268 - 266
		Roadian p5	271 - 268
	Cisuralian P1	Kungurian p4	276 - 271
		Artinskian p3	284 - 276
		Sakmarian p2	295 - 284
		Asselian p1	299 - 295
	Pennsylvanian C2	Gzhelian c7	304 - 299
		Kasimovian c6	307 - 304

Carboniferous C		Moscovian c5	312 - 307
		Bashkirian c4	318 - 312
	Mississippian C1	Serpukhovian c3	327 - 318
		Viséan c2	345 - 326
		Tournaisian c1	359 - 345
Devonian D	Late Devonian D3	Famennian d7	375 - 359
		Frasnian d6	385 - 375
	Middle Devonian D2	Givetian d5	392 - 385
		Eifelian d4	398 - 392
	Lower/early D1	Emsian d3	407 - 398
		Praghian d2	411 - 407
		Lochkovian d1	416 - 411
Silurian S	Pridoli S4	s8	419 - 416
	Ludlow S3	Ludfordian s7	421 - 419
		Gorstian s6	423 - 421
	Wenlock S2	Homerian s5	426 - 423
		Sheinwoodian s4	428 - 426
	Llandovery S1	Telychian s3	436 - 428
		Aeronian s2	439 - 436
		Rhuddanian s1	444 - 439
Ordovician O	Late Ordovician O3	Hirnantian	446 - 444
		Ordovician VI	456 - 446
		Sandbian	461 - 456
	Middle Ordovician O2	Darriwilian	468 - 461
		Ordovician III	472 - 468
	Early Ordovician O1	Floian	479 - 472
		Tremadoc	488 - 479
Cambrian Є	Late Cambrian Є3	["Dolgellian"]	493 - 488
		Paiban	501 - 493
	Middle Cambrian Є2	["Menevian"]	- 501
		["Amgan"]	513 -
	Early Cambrian Є1		520 - 545

Harland et al

Era	Sub-Era	Period	Epoch	Age	when began (mya)

Mesozoic	Triassic		Scythian	Griesbachian	245.0
Palaeozoic	Permian		Zechstein	Changxingian (Tatarian)	247.5
				Longtanian	250.0
				Capitanian	252.5
				Wordian	255.0
				Ufimian	256.1
			Rotliegendes	Kungurian	259.7
				Artinskian	268.8
				Sakmarian	281.5
				Asselian	290.0
	Carboniferous	Pennsylvanian	Gzhelian	Noginskian	293.6
				Klazminskian	295.1
			Kasimovian	Dorogomilovskian	298.3
				Chamovnicheskian	299.9
				Krevyakinskian	303.0
			Moscovian	Myachkovskian	305.0
				Podolskian	307.1
				Kashirskian	309.2
				Vereiskian	311.3
			Bashkirian	Melekesskian	313.4
				Cheremshanskian	318.3
				Yeadonian	320.6
				Marsdenian	321.5
				Kinderscoutian	322.8
		Mississippian	Serpukhovian	Alportian	325.6
				Chokierian	328.3
				Arnsbergian	331.1
				Pendleian	332.9
			Vis�an	Brigantian	336.0
				Asbian	339.4
				Holkerian	342.8
				Arundian	345.0
				Chadian	349.5
			Tournaisian	Ivorian	353.8
				Hastarian	362.5
	Devonian		Upper	Famennian	367.0
				Frasnian	377.4
			Middle	Givetian	380.8
				Eifelian	386.0
				Emsian	390.4

			Lower	Pragian	396.3
				Lochkovian	408.5
	Silurian		Pridoli		410.7
			Ludlow	Ludfordian	415.1
				Gorstian	424.0
			Wenlock	Gleedonian	425.4
				Whitwellian	426.1
				Sheinwoodian	430.4
			Llandovery	Telychian	432.6
				Aeronian	436.9
				Rhuddanian	439.0
	Ordovician	Bala	Hirnantian	Hirnantian	439.5
				Rawtheyan	440.1
				Cautleyan	440.6
				Pusgillian	443.1
			Caradoc	Onnian	444.0
				Actonian	444.5
				Marshbrookian	447.1
				Longvillian	449.7
				Soudleyan	457.5
				Harnagian	462.3
				Costonian	463.9
		Dyfed	Llandeilo	Late	465.4
				Mid	467.0
				Early	468.6
			Llanvirn	Late	472.7
				Early	476.1
		Canadian	Arenig		493.0
			Tremadoc		510.0
	Cambrian		Merioneth	Dolgellian	514.1
				Maentwrogian	517.2
			St David's	Menevian	530.2
				Solvan	536.0
			Caerfai	Lenian	553.7
				Atdabanian	560.0
				Tommotian	570.0
Precambrian	Sinian	Ediacaran	Ediacara	Poundian	580

Acknowledgments:

Harland et al table modified from Stephen E. Jones, The Geological Timescale

ISC html table by Oscar van Vlijmen, Geologische tijdperken (slightly modified)

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page uploaded 28 April 2002
checked ATW030303, last modified MAK110412

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Notes

[1] We use the Russian-Kazakhian stages until the ICS gets around to finally giving these Early Cambrian ages some names. As of this date (041118), the ICS Early Cambrian Epoch is undivided.

[2] We use *chaotic* in its mathematical sense, meaning that the end state of a closed system is extremely sensitive to initial conditions. The classical example is from meteorology, in which the occurrence of a hurricane is supposedly determined by the wing beat of a butterfly six months earlier and ten thousand miles away.

[3] These peculiar names are English corruptions of French corruptions of Micmac (Amerind) place names. Escuminac and Miguasha actually have very pedestrian meanings: "Lookout Point" and "Red Cliff," respectively, thus proving that the original inhabitants were just as unimaginative as the French and Tory settlers who replaced them.

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The Cambrian: 1

The Cambrian Period of the Paleozoic Era: 542 to 488 Million Years Ago

All these pages are currently still being revised

The Cambrian: 1

The Cambrian Period of the Paleozoic Era: 542 to 488 Million Years Ago

Introduction

The first eon of Earth's history, from the first coalesence of the planet, about 4500 Mya, to about 542 Mya, is referred to as the Precambrian. From this hint, one might well suppose that the Cambrian comes next -- which it does, in a way. Actually, this is the biggest break point in all of geology. It marks the beginning of the Phanerozoic Eon, the Paleozoic Era, the Cambrian Period, the Terreneuvian Epoch, and the Fortunian Age (the first age of the Cambrian). The Cambrian Period was named in 1835 by the geologist Adam Sedgwick, after the region of Cambria in North Wales, where rocks of this age were first found. The name "Cambria" is a version of *Cumbria*, a latinisation the Welsh *Cymry* (= countryman, compatriot against the invading Anglo-Saxons).

A mid Cambrian scene, a reconstruction of the famous Burgess Shale site in what is now British Columbia, Canada. In the foreground a swimming *Laggania cambria* has captured a hapless trilobite. On the sea floor from left to centre respectively are a solitary specimen of the proto-annelid *Wiwaxia* and three specimens of the lobopod *Hallucigenia*. Note in both animals the defensive array of spines. Further to the right is the lobopod *Aysheaia* with its anterior prongs around the mouth, as well as the protoarthropod *Opabina*, a close relative of *Laggania.* Descending to the sea floor are two individuals of the basal arachnomorph *Marrella*. Also visible in this scene are sessile epifauna in the form of the deuterostome *Dinomischus* (yellow) and the hexactinellid sponge *Vauxia* (blue). Image and (modified) caption from here. Image originally from **The Crucible of Creation** by Prof. Simon Conway Morris.

Long before it was a formal stratigraphic unit, the Cambrian was a concept about Earth history. It was understood to be the earliest period in which one could find the fossils of multi-celled animals (Metazoa). Since then, metazoans and their fossilized traces have been found well before 550 Mya. In particular, Ediacarans, a group of very strange and poorly understood creatures -- but obviously metazoans -- have been found in many parts of the world with ages pushing the 600 Mya mark.

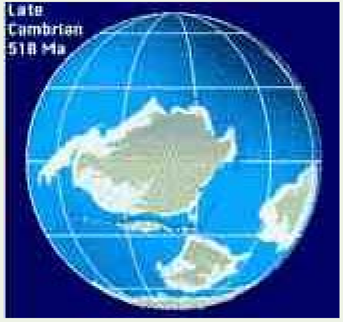
Consequently, paleontologists now view the Cambrian as the period when the Bilateria first appeared and, almost at the same time, the first metazoans with shells. The Bilateria include all living metazoans except jellyfish, corals, and sponges. Bilaterians have a head at one end of an elongate body which is bilaterally symmetrical (hence the name). Their embryos all develop a separate layer of embryonic cells, called mesoderm, between the gut or coelom and the outer wall of the animal. If this whole description suggests a worm, you've got the right idea. A flatworm is the most basal living form of bilaterian.

Unlike many other, somewhat arbitrary, geological markers, the base of the Cambrian Period is defined with reference to the underlying paleontological concept. Small worms rarely leave body fossils, but their burrows are frequently preserved. The burrows of bilaterian worms are fairly distinctive. Trace fossils are often given names as if they were organisms, and the earliest well-known bilaterian trace fossil is a type of fossilized burrow referred to as *Treptichnus pedum*. The base of the Cambrian is currently defined as the first occurrence of *T. pedum* at Fortune Head, near the town of Fortune, on the north coast of western Newfoundland, Canada.

Paleogeography and Tectonics

The Cambrian period saw most continents located in the southern hemisphere at low paleolatitudes (near the equator). The Ediacaran supercontinent of Pannotia continued to assemble in some regions but fragmented into Gondwana Laurentia, Baltica, and various mostly submerged Asian blocks.

Laurentia stretched across the Cambrian equator, partly submerged by the Iapetus ocean, with a mostly mostly submerged Baltica and Siberia approaching from the South-East.



Gondwana remained the largest supercontinent. Other continents included Kazakhstania and China (actually China, Thailand, Malaysia, and Indochina). Seas were for the most part shallow, especially along the edges of the continents.

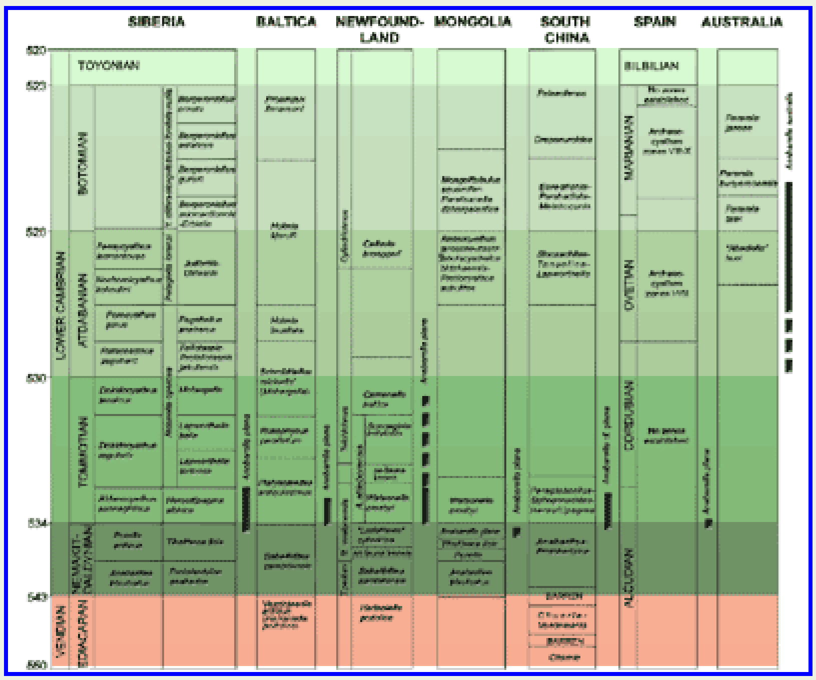
Global (eustatic) transgressions occured in the Middle and Late Cambrian, as shallow seas repeatedly invaded the land, providing a perfect habitat for many types of marine invertebrates. These shallow epeiric seas covered much of the continents except for Gondwana, where there were highlands. Other highlands could be found in Eastern Siberia and Central Kazakhistan.

Maps:

- Cambrian and Latest Precambrian
- Cambrian: the beginning of the Paleozoic Era

Stages of the Cambrian

Current Status of Early & Middle Cambrian Stratigraphy



The stratigraphy of the Cambrian -- particularly the Early and Middle Cambrian -- has always been chaotic. A brief survey of recent work suggests that it is likely to remain that way. The ICS has outlined its proposal for these epochs, but it has been impossible to obtain concensus. The heart of the problem lies, not with some innate intractability of the stratigraphic psyche, nor with administrative bungling by the ICS. The source of the confusion is, rather, the creativity of stratigraphic science.

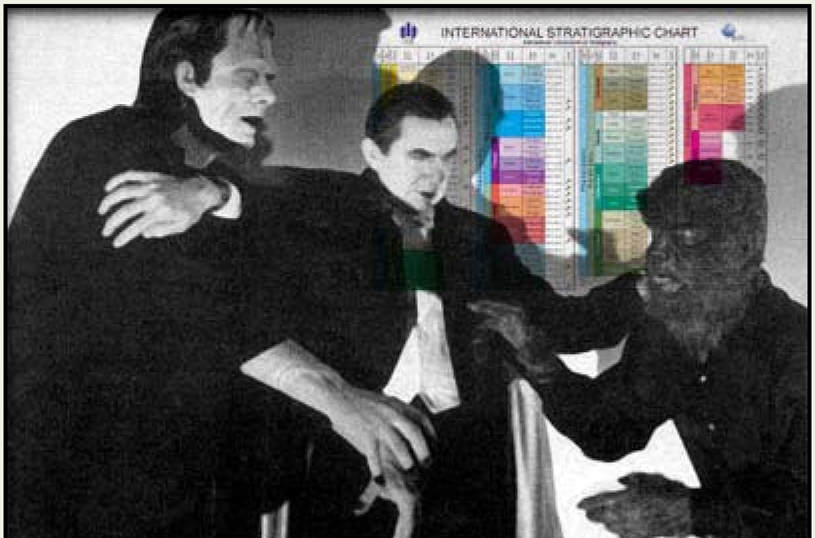
In the XIXth and XXth Centuries, the Lower Cambrian could not be subdivided with any confidence because none of the usual markers were present. There were few well-mapped Early Cambrian sites, and no Early Cambrian conodonts, ammonites, graptolites, readable magnetic polarity reversals, or even (thankfully!) any iridium anomalies. Nevertheless, the problem in the XXIst Century is the opposite. We are now awash in data from new sources using new methods which have not been adquately standardized, correlated in different regions, or securely nailed down with radiometric dates.

One excellent example is the base of the Cambrian itself. Only a few years ago, the stratigraphic community coalesced around the idea that, although there were essentially no Earliest Cambrian fossils, except the unclassifiable Ediacaran fauna, the Cambrian should begin with the first macroscopic trace fossils -- simple bioturbation by bilaterian "worms." In 1992, the ICS selected a suitable global stratotype section and point in Newfoundland, Canada, to mark the first clear appearance of bilaterian animals at about 542 Mya. Now (2006), only 14 years later, it is obvious that the Bilateria date well into the Ediacaran, as evidenced by fossils like *Kimberella* (Fedonkin & Waggoner, 1997), bilaterian, possibly arthropod, trace fossils (Martin *et al*., 2000), and -- yes -- even trace fossils of bilaterian worms (Dornbos *et al*., 2005).

Meanwhile, new, but rather unstandardized, stable isotope techniques (*e.g.* $^{87}Sr/^{86}Sr$, $d^{13}C$) have added layers of new stratigraphic information. *See*, *generally*, Knoll (2000) (we, too, have had a shot at explaining $d^{13}C$ measurements and discussing some of their problems). Previously "enigmatic" Ediacaran and Early Cambrian fossils are also being gradually tied to conventional taxa, so that biostratigraphic schemes and correlations can be extended into previously dark corners of the Cambrian. Knoll (2000). For examples, *see* Jago *et al*. (2002); Gubanov & Peel (2003). Finally, as in many other areas of paleontology, political changes in the last two decades have opened new localities to exploration (and closed others).

Consequently it has become possible to create rather elaborate biostratigraphic correlation charts, such as the one shown here, adapted from Gubanov & Peel (2003). Click on the chart to see a larger, almost legible, version. As in many such studies, Gubanov & Peel have used the Russian (Siberian Platform) stage names for the Early Cambrian ages. However -- and also as in most such studies -- the absolute dates developed by Gubanov& Peel for these presumptive Early Cambrian stages bear little resemblance to the ICS scheme.

The ICS Position



The Cambrian Working Group striving for consensus

Meanwhile, the International Subcommission of Cambrian Stratigraphy (ISCS) at the ICS has been, ever so slowly, working away at the insurmountable problem of imposing an "official" stratigraphy on ground which is both literally and figuratively shifting. On one side, they face increasing pressure and high-volume whining from ill-mannered people, including ourselves, who need a stable, well-characterized outline for the Cambrian. On the other side lies the abyssal certainty that, whatever they decide, it will be obsolete within a few years and everyone will laugh at them. So, like Frankenstein (who was sort of a committee himself) the ISCS has slowly retreated before an angry mob of geological peasants armed with with torches and pitchforks, shuffling up the narrow mountain defile towards an inevitable doom. Occasionally, the ISCS howls with rage and frustration, and tosses down a partial decision or two to discourage the more aggressive challengers.

In this curious manner have we made halting, and somewhat limited, progress toward an official stratigraphy of the Cambrian. Actually, a comparison of the annual reports of the ISCS for **2001** and **2005** suggests that not a lot has been accomplished in the last few years, and the **ISCS website** is in serious disrepair. Nevertheless, the promises made by the Subcommission have at least become much more specific, due largely to actions taken in the last year (2005).

Here's the current status. The Early Cambrian will be divided into two epochs ("series"), each containing two ages ("stages"). The earlier of the two epochs is the Terreneuvian. The general effect is to collapse the top of the Early Cambrian into the Botomian (!). The Middle Cambrian and Furongian will each have *three* ages. The impact of tripartite divisions is hard to assess, since almost every regional system uses only two stages for each of these epochs. The ISCS has picked out some likely trilobites to mark these later stages. Thus, we expect that all this will be filled out with trilobite zonation in the fullness of time.

For the lower reaches of the Cambrian, the obvious and sensible thing would be for the ISCS to adopt the stages from the Siberian Platform, like everyone else. The probability that this will happen approaches zero. However, this type of decision sometimes becomes an intensely political business. We try our best to steer clear of political issues. Accordingly, we will refrain from further comment or speculation. The current (2008) overall picture looks like this:

Period	Epoch	Age	Informal Name	Base Date	Duration (My)
Ordovician	Early Ordovician	Tremadoc		488	9
Cambrian	Furongian	Cambrian X	Dolgellian	~492?	4?
		Cambrian IX		~496?	~4?
		Paiban	Maentwrogian	499	~3
	"Middle Cambrian" Cambrian Epoch 3	Guzhangian	Menevian	~503	~4
		Drumian	Late Amgan	~507	~4
		Cambrian V	Early Amgan	~510?	~3?
	Cambrian Epoch 2	Cambrian IV	Botomian (including Toyonian)	~517?	~7?
		Cambrian III	Atdabanian	~521?	~4?
	Terreneuvian	Cambrian II	Tommotian	~528?	~7?
		Fortunian	Nemakit-Daldynian, or Manikayan, Manykajan, etc.	542	~14
Ediacaran (ICS)				~630	~88

The '~' indicates an estimated date or duration, while '?' indicates unofficial status of the underlying stage.

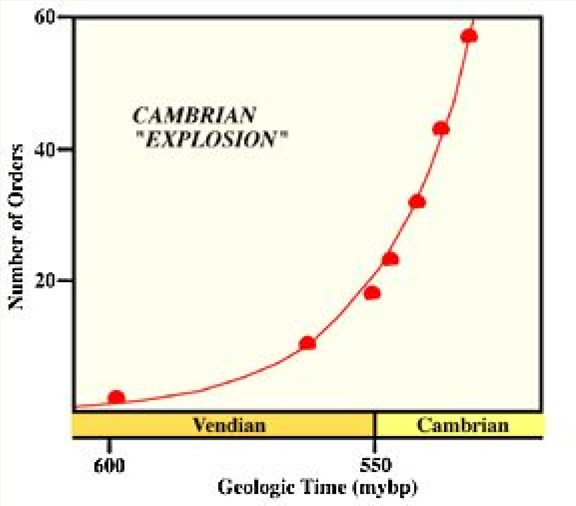
As we write (2008), there is furious re-dating going on, with some boundaries (e.g. Tommotian, Paiban) seeming to change from month to month. Thus, while we are current to a certain point, the dates may be slightly obsolete by the time you refer to this page. While this is awkward, it is a distinct improvement over the stasis of the pre-2006 era. ATW080426

Climate

The Cambrian climate was generally warm, wet and mild. As there were no continental landmasses located at the poles, ocean currents were able to circulate freely, hence there was no significant ice formation. As a result temperatures worldwide were mild. The Cambrian constituted a benign spell between two great ice ages - the late Proterozoic Snowball Earth and the Late Ordovician Ice Age.

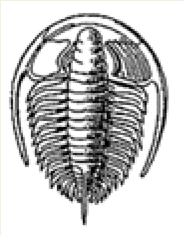
Life - the Biosphere

At the beginning of the Cambrian period, about 540 million years ago, life was entirely confined to the oceans. During the 53 million years that the Cambrian period lasted there was the sudden appearance and diversification of almost every major group (phylum) of animal life, as well as many types that later died out.



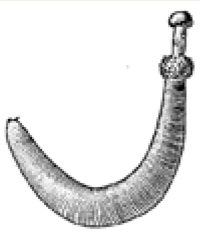
Animals with shells and exoskeletons appeared for the first time, including trilobites, brachiopods, molluscs, and many other groups. This sudden evolutionary burst was so spectacular that it has been termed the "Cambrian explosion". There hasn't been anything like it on Earth before or since.

The most characteristic animals of the Cambrian period were the trilobites, a primitive form of arthropod remarkable for it's highly developed eyes (unusual in such an early organism).



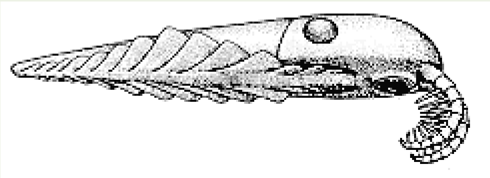
The trilobites appear suddenly during the Atdabanian epoch (several groups are known, including large spiny types and small planktonic forms), reached their fullest development in the middle Cambrian and the following (Ordovician) period, and gradually declined after that and became extinct by the end of the Paleozoic era.

Other very important groups of Cambrian animals were the sponges, echinoderms (represented by a large number of different classes), and most interesting of all the soft-bodied echiurians, which were burrowing worm-like creatures (see right), which seemed to have been the most important and predominant carnivores of the time.



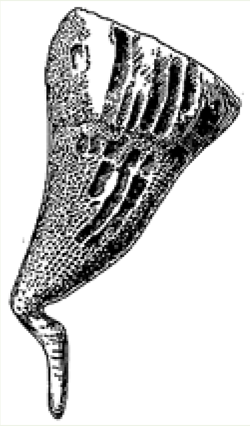
The earliest gastropods (marine snails) also appeared in this period, as did the cephalopods (during the Furongian) and other now extinct lineages of Molluscs. Molluscs however were still relatively rare, they did not become an important element of the marine fauna until the Early Ordovician period.

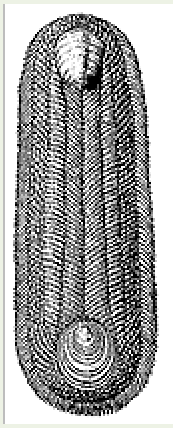
The first chordates (vertebrate ancestors) occurred as did the first foraminifers (shelled amoebas).



Many Cambrian creatures however did not fit into modern categories of organisms; they seemed to have been representatives of unknown or experimental phyla.

Greatest of all the Cambrian beasties were as the Anomalocarids. Shown here is *Laggania cambria*. Averaging 45 to 60 cm, with exceptional specimens reaching 1 or even 2 metres, these animals dwarfed even the largest trilobites. They were armed with twin grasping organs and a wicked mouth with a ring of teeth in shape rather like a pineapple slice. Many trilobite exoskeletons have been found with large bites taken out of them, the result of an encounter with *Anomalocaris*. Like the shark of today, *Anomalocaris* . was perfectly adapted to its environment, and a single species existed without change for some 30 million years or more. Scientists do not agree what group of modern creatures *Anomalocaris* was most closely related too. Suggestions most often include arthropods, but the aschelminthe group of worm-like creatures is another possibility. I am wary of pigeonholing extinct organisms with living types on the basis of superficial similarity. Like many Cambrian creatures, *Anomalocaris* is best put in a phylum of its own.



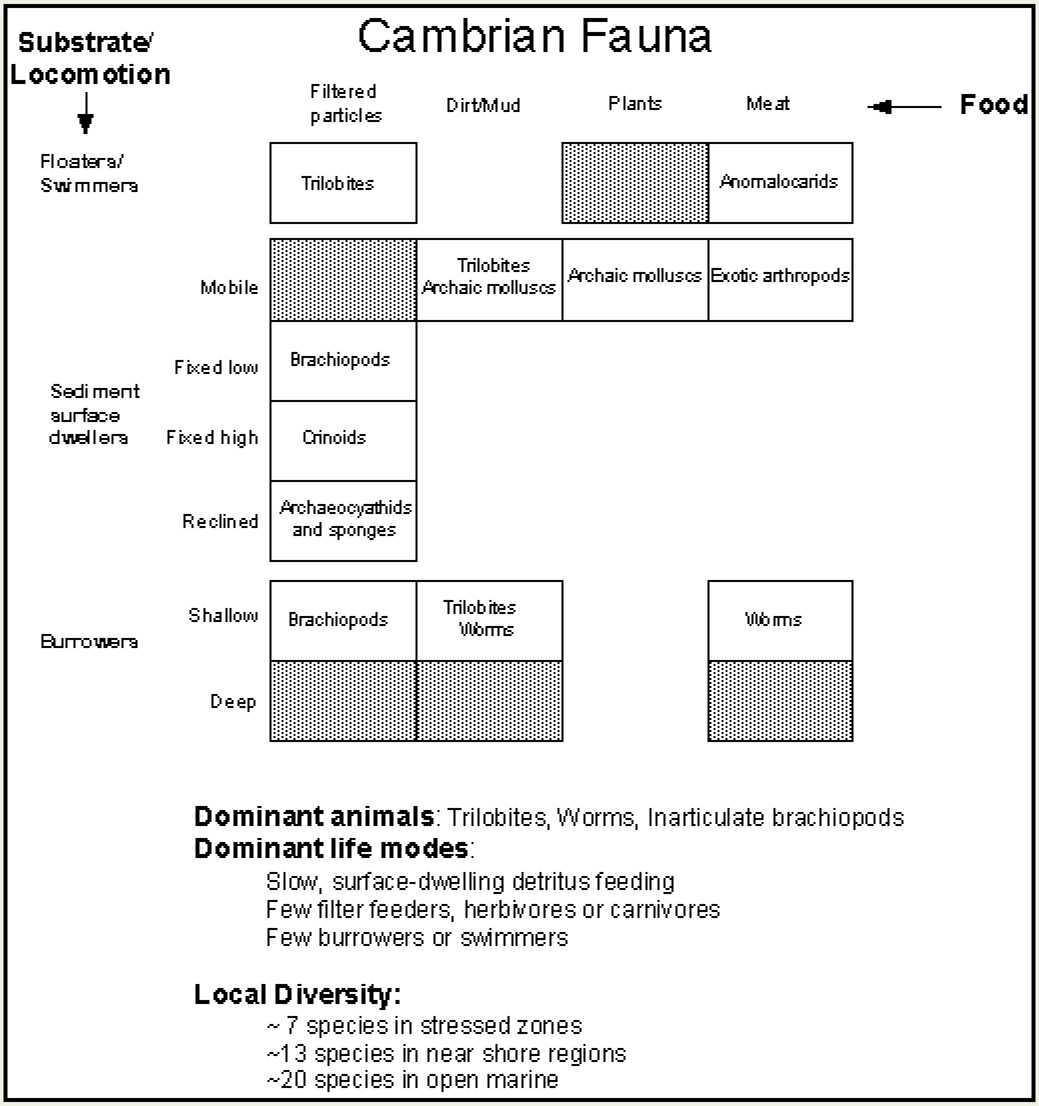


Halkeria is one of a number of the strange armoured "coat of mail" creatures that inhabited the early Cambrian oceans. The specimen shown here is about 3.5 cm in length. In addition to the calcareous scales it possessed two mollusc-like limpet-shaped shells. Later forms such as the Middle Cambrian *Wiwaxia* lost the shells and developed long spines instead. It is not certain that these strange creatures even are molluscs, although a radula-like structure has been found in *Wiwaxia*. Jan Bergström suggests that they represent a group of late surviving "Procoelomates", the ancestors of all higher (Coelomate body plan) animals.

The enigmatic sponge-like cup-shaped archaeocyaths (*left*) were very common during the early Cambrian, forming great reefs, but died out almost completely by the middle of the period, leaving no descendents.

Plants of the Cambrian period included only algae (seaweeds). There were no known land plants, the land was still bare of any life other than microorganisms.

The Marine Ecosystem



Cambrian Ecosystems did not seem to have been as robust as those of later times, perhaps due to the smaller diversity. Cambrian communities were loosely organized and considerable experimentation and morphological flexibility were features of many assemblages (Hughes, 1994). Cambrian Lagerstätten such as the Burgess Shale contain a wide range of apparently morphologically disparate organisms. "The period saw a number of mass extinctions and radical turn-overs of life. By far the most serious was the Botomian turnover, which, in terms of percentage of overall diversity lost, was even more severe than the end Permian extinction. Most Small Shelly Animals were wiped out, as were the majority of archaeocyaths and the worldwide archaeocyath reefs

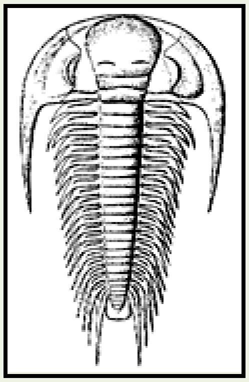
The Latest Botomian (Toyonian) fauna represented a more traditional trilobite-brachiopod dominated Cambrian ecosystems. But even here there were a number of extinction events that took a toll on the marine fauna, During the Furongian alone, there were three distinct bio-stratigraphic intervals in trilobite distribution, each marked by a mass-extinction. The cause of this is not clear, but it may have been related to climate change, as most genera affected were warm water species.

Following the earliest Cambrian (Tommotian) fauna, there was a rise of herbivore grazers (e.g. gastropods), and consequent decline of algal stromatolites . There were almost no large animals, and only a few predators (chiefly anomalocaridids).

Cyanophyte algae mats encouraged mat scratchers (diverse ancestral mollusks, esp. diverse monoplacophorans and polyplacophorans), and some probable mat-sticking echinoderms (helioplacoids).

Most life concentrated near sediment- water interface; with only shallow burrowers and encrusters. Even so, the Cambrian benthos had already developed a simple tiering system with two levels of (0-50 mm and 50-100 mm. The lower tier was dominated by archaeocyaths, which formed small reefs (in the Terreneuvian and Cambrian Epoch 2 only: there were almost no Middle or Furongian reefs), echinoderms, nonarticulate brachiopods and sponges; the higher level included archaeocyaths, echinoderms (eocrinoids and crinoids) and were rare but nevertheless included some bizarre forms such, as the helicoplacoids. Most Cambrian echinoderms were stalked (and thus sessile), but some were motile (able to crawl about)

The Cambrian saw the beginning of bioturbators, with limited vertical mining abilities. This infauna was generally shallow, burrowing close to the sediment-water interface with the exception of vertical *Skolithos* burrows, which were often deep.



Trilobites dominated the mobile benthos, accounting for over 50% of Cambrian hard-shelled species. In many exposures, over 90% of the fossils recovered are trilobites. Benchley & Harper (1998). However, note that, the fact that trilobites are the most common fossil doesn't necessarily mean that trilobites were the most common animal. Trilobites had a hard carapace, molted frequently, and hence they left a disproportionately heavy fossil record compared to other creatures living at the same time. These trilobites were mostly benthic epifaunal detritovores (possessing a backwards facing mouth). That is, they were detritus-feeders crawling across or swimming above the sea-floor. Other species may have lived in shallow burrows. Both body and trace fossil representatives of the trilobites are common in Cambrian strata. They are known from many growth stages, thousands of species, and trace fossils. The functional morphology of the Furongian olenids indicates the already sophisticated design of the Cambrian Trilobita.

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Brachiopods included "inarticulates"; both linguates (infaunal forms with calcium phosphate shells) and craniids epifaunal forms with calcite shells). Articulate brachiopods (epifaunal with calcite shells) are present but rare.

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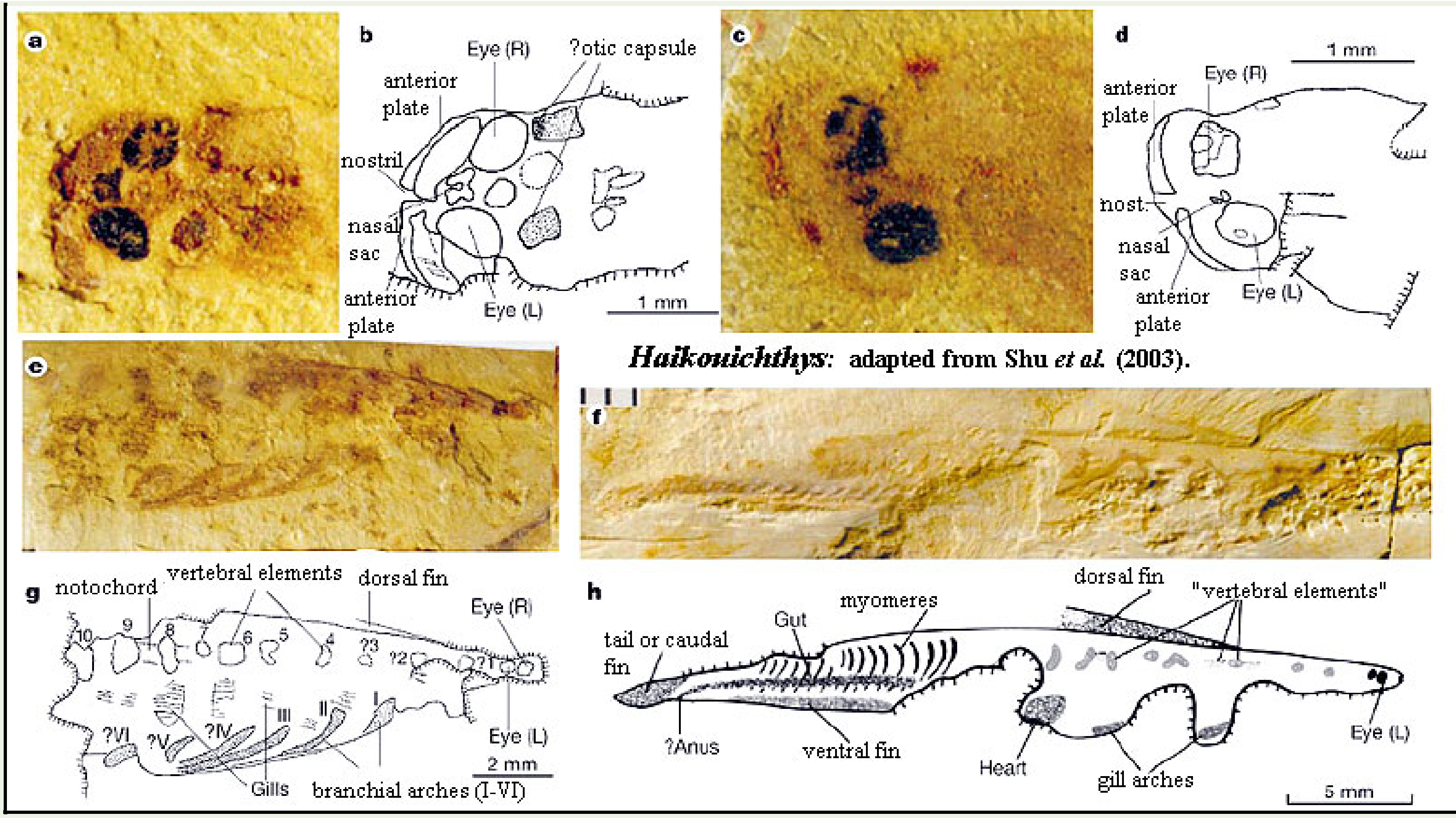
The Cambrian: 2

Vertebrates

The main issue concerning Cambrian vertebrates is whether there were any. It seems likely that at least one lineage of vertebrates existed before the Ordovician, but the issue is not entirely settled. Two organisms in particular are possible Cambrian vertebrates: *Haikouichthys* and *Anatolepis*. In addition, two other vertebrate lineages are ancient enough that it would be reasonable to suppose they originated in the Cambrian, even without a clear fossil record: conodonts and thelodonts.

Haikouichthys was originally described by Shu *et al*. (1999) as one of two possible vertebrates on the basis of unique specimens from Chengjiang. The other specimen, *Myllokunmingia*, remains unique. It has also been suggested that *Myllokunmingia* is the same as *Haikouichthys*. Hou *et al*. (2002). However, the issue of *Myllokunmingia*'s exact characteristics and affinities became somewhat less urgent since, shortly thereafter, *five hundred* new specimens of *Haikouichthys* were found near Haikou. Portions of the anatomy were then redescribed on the basis of this massive body of new data by an all-star cast of Chinese and Western early vertebrate specialists. They pronounced *Haikouichthys* to be a certifiable vertebrate on the basis of numerous characters. Shu *et al*. (2002). We hasten to add that this does *not* place *Haikouichthys* in the Vertebrata, as we use that term in the Vertebrate section of Palaeos. To the contrary, the cladogram of Shu *et al*. (2003) identifies *Haikouichthys* as a basal chordate, or possibly a basal craniate (hags > hagfish), but not a vertebrate (vampires > lampreys). Nevertheless, Haikouichthys has a number of characteristics thought to be vertebrate synapomorphies.



***Haikouichthys*: adapted from Shu *et al.* (2003).**

For those with an interest in conodonts, note how wonderfully this interpretation of *Haikouichthys* squares with our heterodox interpretation of the conodont cranium. One more organism of this sort, and we'll actually start taking ourselves seriously...

By contrast, *Haikouella*, originally thought to be a stem vertebrate, is now regarded as a Vetulicolian or other stem deuterostome. Shu & Conway Morris (2003) have made a point of "emphatically contest[ing]" the vertebrate affinities of *Haikouella*, emphasizing the absence of eyes, notochord, myomeres, or brain.

Links

LINKS

Websites

The Cambrian Period, at the University of California Museum of Paleontology. **best on the web**

The Cambrian World - Stratigraphy - Localities - Life in the Cambrian

The Cambrian Period - good essay, from from **Peripatus**

The Cambrian Period - Dr Pamela Gore - some useful study notes, complete with links and a few photos of several types of trilobite. An excellent introduction, if you don't mind the Geology 102 format. Includes material on the famous Burgess Shale site.

American Scientist: January-February 1997 - Origin of Animal Body Plans - explains how multicelluar animals suddenly appeared during the Cambrian, after billions of years of nothing but micro-organisms

MSN Encarta - Cambrian Period - Short entry, summarizes the life forms and geologic activity that mark this time period.

Books

Wonderful Life : The Burgess Shale and the Nature of History by Stephen Jay Gould - classic work on early Metazoan evolution, also historic overview of the discovery of the Burgess Shale fauna. Argues that many Burgess Shale remains belong to extinct phyla with no know relatives. Raises some interesting philosophical questions on the evolution of life. Some of Gould's claims have since been refuted in the light of subsequent research (e.g. *Hallucinagenia* has turned out to be a lobopod), but he still makes many valid points.

The Crucible of Creation : The Burgess Shale and the Rise of Animals by Simon Conway Morris, - a very facscinating and readable alternative to Gould - argues that rather than a bush of many unrelated extinct lineages, these ancient organisms all fit together on an evolutionary tree. My own stance is probably somewhere between that of Gould and Morris

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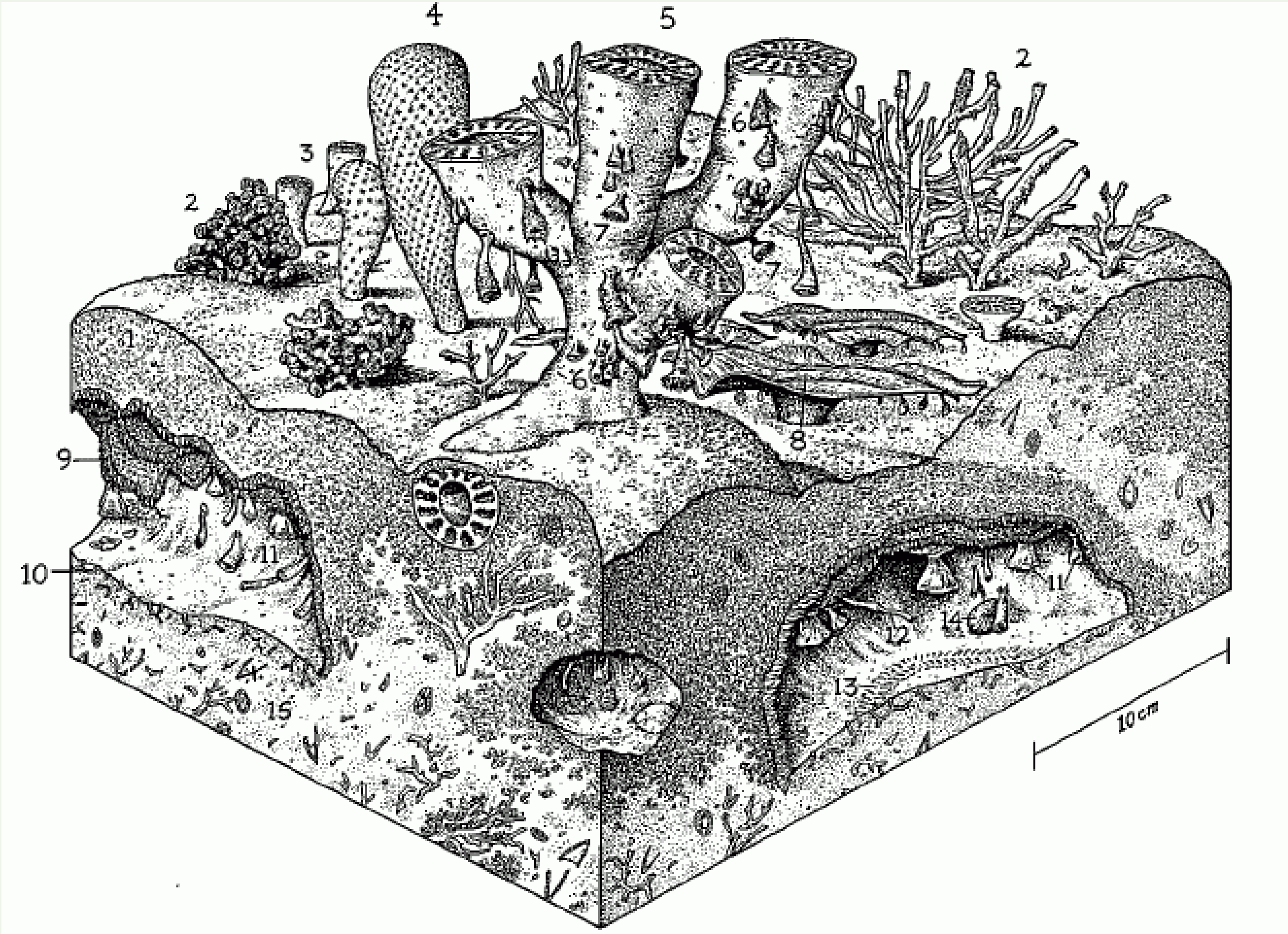
The "Early Cambrian" Epochs:1

The Terreneuvian Epoch and Cambrian Epoch 2 of the Cambrian Period: 542 to ~510 million years ago



Reconstruction of an Early Cambrian reef community (from 97). 1. *Renalcis* (calcified cyanobacterium); 2: branching archaeocyath sponges; 3: solitary cup-shaped archaeocyath sponges; 4: chancellorid (?sponge); 5: radiocyath (?sponge); 6: small, solitary archaeocyath sponges; 7: cryptic "coralomorphs"; 8: *Okulitchicyathus* (archaeocyath sponge); 9; early fibrous cement forming within crypts; 10: microburrows (traces of a deposit-feeder) within geopetal sediment; 11: cryptic archaeocyaths and coralomorphs; 12: cryptic cribricyaths (problematic, attached skeletal tubes); 13: trilobite trackway; 14: cement botryoid; 15: sediment with skeletal debris.

Rachel Wood - The Ecological Evolution of Reefs (also R. A. Wood, 1998. Reef Evolution.

Introduction: A Time of Radical Change

This was a time of great change across a wide spectrum, from tectonic (the breakup of the early Rodinia and Pannotia supercontinents) through geographical (marine transgressions as the ocean invaded the land creating shallow continental seas that allowed primitive life to flourish), atmospheric, (rising oxygen and falling carbon dioxide levels), biogeochemical (changing ocean chemistry, promoting biomineralization; especially the upwelling of high phosphorous levels (large phosphorite deposits), enabling organisms to develop skeletons of calcium phosphate), and ecological (the appearance of predation and algae grazers, which meant an end of the Ediacaran idyll). This combination of events would seem to have been responsible for the sudden and remarkable and diversification of metazoan life at this time.

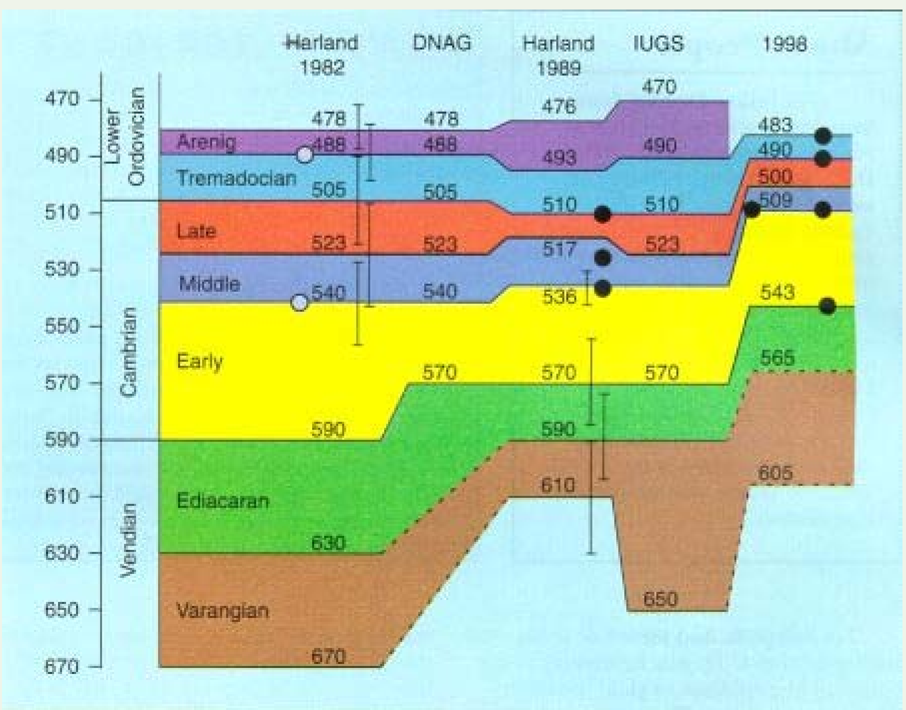
The Early Cambrian was a time of incredible diversification. Quite possibly, this process had begun earlier, but the fossil record first reveals the results during this relatively brief interval of 30 My or so. It seems to have proceeded in three stages, sometimes referred to by the names of three Siberian Cambrian stages: the Manykian, Tommotian and Atdabanian. At the beginning of the epoch, we have simple worm traces, followed shortly by tiny,rather simple shells, the so-called "Small Shelly Fauna" of the earliest Cambrian, or Manykian Age. This was followed by a much more diverse group of shelly animals often referred to as the Tommotian fauna. The relationships of Tommotian animals to living groups are not understood, but it is likely that mollusks also evolved at this time. The Tommotian animals disappeared rather quickly and were followed by the "Cambrian Explosion" of modern groups in the last half of the Early Cambrian (Atdabanian Age). By the end of the Early Cambrian, almost all of the modern phyla had evolved: mollusks, annelid worms, arthropods (including the trilobites), echinoderms, and chordates, to name but a few.

Thus, in the space of about 17 My, roughly from 530 to 513 Mya, the pattern was set for almost all subsequent macroscopic animal life. Many writers have marveled at the amount of new diversity. Stephen Gould�s popular book on the Burgess Shale, of the Canadian Middle Cambrian, **Wonderful Life**, celebrates this explosion in some detail. Gould (1989). What we are now learning is even more startling -- the extraordinary *durability* of this new diversity. Since this was the first radiation of metazoans, its not really surprising that this new life form, expanding into an ecological vacuum, should produce many new varieties. What is a bit harder to explain is why so many of these animals reflect groups which survived for hundreds of millions of years. Most explosive radiations seem to generate a lot more in the way of unsuccessful early models. Perhaps these forms were weeded out in the Manykian and Tommotion Ages. Then again, perhaps we just haven�t found enough fossils yet. The remarkable fossils of Chenjiang, of latest Early Cambrian age, are just now being described in detail. These fossils may eventually give us an entirely new perspective on this key period of early metazoan life.

We do know that the seas rose continuously throughout the Early Cambrian. Higher water is almost always good for life, and this was particularly true during the Paleozoic. Here�s why. The deep oceans are not very useful for life. Plants and photosynthetic bacteria form the base of the foodchain everywhere. Only the top 100 meters or so of the deep oceans are reached by light and can support these organisms. In addition, the deep oceans provide no substrate for plants to attach and get big. However, when the seas rise, they spill over the broad flat coastal plains of the continental shelves. Thus, a small rise in sea level means a lot more area covered by water. This new area of continental sea is shallow -- almost all of it within the "photic zone" in which plants can live. These sunlit continental seas also provide a substrate on which photosynthesizers can attach and grow large. Thus even relatively small increases in sea level can have huge effects on the productivity of the oceans.

Shallow seas also provide a substrate for reef-builders. We tend to think of coral or oyster reefs as picturesque, ecological reservoirs of diversity confined to a relatively small band of tropical waters. But we live in a very unusual corner of Earth history. By comparison with most of the Phanerozoic, our age is bitterly cold and dry. In many, more typical portions of planetary space-time, the shallow seas were almost all warm and dominated by vast reefs which formed complex three-dimensional marine arcologies in wide belts extending for of hundreds, or even thousands of kilometers along the ancient coasts. The Early Cambrian saw the first large reef complexes of this type, although they would be unimpressive by Mesozoic standards. The reef-builders of that epoch were the lacy, vase-shaped archaeocyaths, probably related to sponges, along with other organisms whose affinities are not yet understood.

Age of the Early Cambrian



Age estimates of the Ediacaran, Cambrian, and Early Ordovician

International Subcommision on Cambrian Stratigraphy

Around 1990 it became evident that most of the published radiometric data on the Cambrian were based on Rubidium-Strontium, which gave ages that were up to 50 million years too high. This created a series of drastic revisions, in the age assignment of the Cambrian in general, and especially its lower boundary as shown in the above figure (for more detailed information see Cambrian Stratigraphy) Overall the presumed length of the Cambrian has been reduced from almost 100 million years to little more than half of that. However, it can be seen that the Early Cambrian (yellow band in this diagram) takes the lion's share and in fact remains a longer interval than both the Middle and Late Cambrian combined.

Subdivisions

The Cambrian of the Siberian Platform and adjacent areas are among the best studied Cambrian sequences, and the traditional Siberian Early Cambrian stages (Tommotian, Atdabanian, Botomian, Toyonian) are often used for global comparisons although no formal decision has been made. In in 1992 the Nemakit-Daldynian, now called the Fortunian Stage, was added for the most basal strata, preceeding the Tommotian. The entire series is shown in the table here.

Early Cambrian Life

> During the first 10 million years of the Cambrian Period the Tommotian fauna was replaced by a more diverse biota of larger metazoans participating in more complex communities. The Cambrian fauna was dominated by low-level suspension feeders such as the nonarticulate brachiopods and eocrinoids together with monoplacophoran and hyolith mollusks. Two parazoan groups developed colonial strategies: the archaeocyaths and possibly the sponges. Colonies tend to develop iteratively with new iterative units or modules derived by continuous growth from existing units. The colonial or iterative body plan thus contrasts with the unitary or solitary life mode of most organisms. A number of groups show clear trends towards a greater integration of individuals within the colony and in some cases a differentiation of functions across the colony.

Benchley & Harper (1998).

MAK020516.

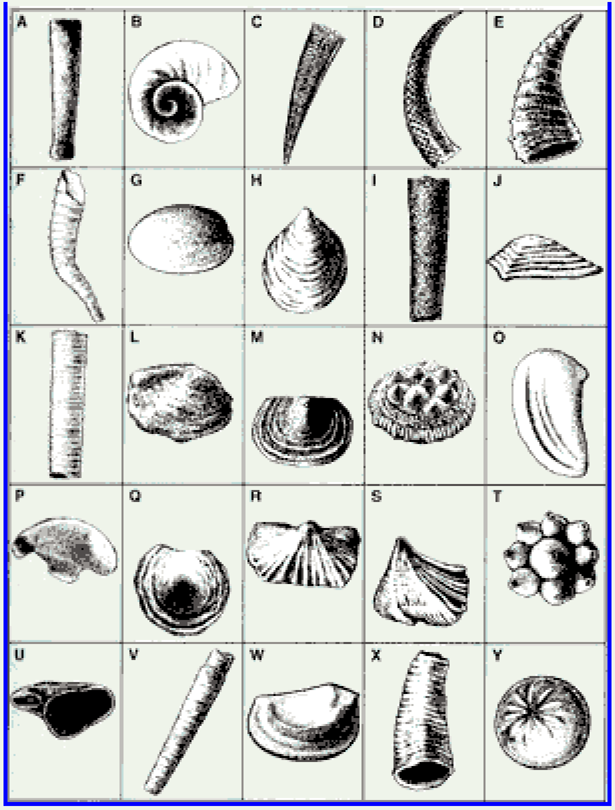
The Small Shelly Fauna

Notes from the literature:

Runnegar (1992):

> [S]tudies of Cambrian fossiliferous strata in Siberia, China, Europe, and Australia have yielded an unexpected range of well-preserved phosphatic microfossils. Most are either tiny shells or the disarticulated components (sclerites) of a protective armour comprised of many parts (Bengtson *et al.*, 1990). These microfossils have become familiar as the "small shelly fossils." Most are original phosphatic skeletons or phosphatic copies of other kinds of hard parts ... .

> Stimulated in part by an international endeavour to define the Precambrian-Cambrian boundary for the global geological time scale, studies of Cambrian fossiliferous strata in Siberia, China, Europe, and Australia have yielded an unexpected range of well-preserved phosphatic microfossils. Most are either tiny shells or the disarticulated components (sclerites) of a



protective armour comprised of many parts (Bengtson *et al*., 1990). These microfossils have become familiar as the "small shelly fossils." Most are original phosphatic skeletons or phosphatic copies of other kinds of hard parts ... .

Grotzinger et al. (1998) (abstract):

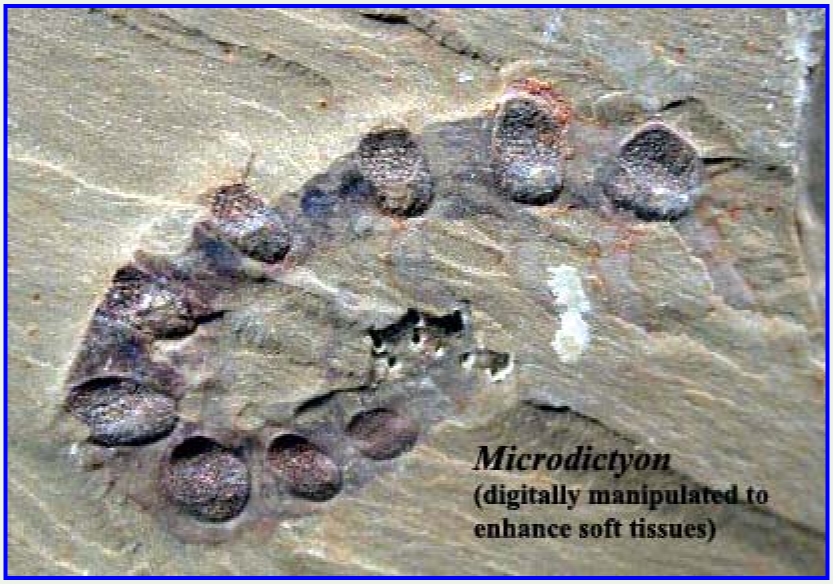
Abundant calcified fossils occur in the terminal Proterozoic Nama Group, Namibia. The fossils are constrained to occur stratigraphically below the first occurrence of *Phycodes pedum*, overlap in range with known Ediacaran fossil impressions, and extend between ash beds dated at 549 and 543 Ma. At least six distinct morphotypes have been identified to date, suggesting that the proportional representation of calcareous taxa in the terminal Proterozoic fauna was not markedly different from that observed in younger periods. New taxa include branching forms up to 1 cm in diameter that display hexagonal symmetry. This symmetry recalls the tri-radiate geometry of several prominent terminal Proterozoic and basal Cambrian taxa, including *Tribrachidium* and *Anabarites*. Other forms include open cups possibly representative of simple asconoid (vase-shaped) sponges; simple tubes that are functionally (if not necessarily phylogenetically) comparable to sabellid worm tubes, possibly indicating the presence of anterior tentacles or lophophore-like appendages; and more complex multichambered forms. In terms of abundance, the simple cups and tubes are most numerous, followed by the complex branching and multichambered forms, and then the previously described *Cloudina*. All calcified fossils in the Nama appear to represent benthic organisms that lived in close association with thrombolitic and stromatolitic reefs and biostromes, suggesting a strong substrate preference. Generally, they are rare or absent in other facies. Although the forms with hexagonal symmetry may be related to *Anabarites*, most Nama calcareous fossils disappear near the PC-C boundary and do not appear to be closely related to Cambrian small shelly fossils. For the most part, they are as enigmatic as the canonical Ediacaran biota.

Haas (1981) paraphrase:

Small shelly fossils near the base of the Cambrian mark the transition to a skeletonized fauna and the metazoan-dominated Phanerozoic fossil record. The recovery of articulated specimens composed of multiple sclerites discussed above, such as *Wiwaxia, Halkieria* and *Microdictyon*, suggests that much of the remaining "small shelly fauna" represent elements similarly employed as ectodermal armor in bilaterian Metazoa that have yet to be recovered in an articulated form. In addition, recent finds of cap-shaped shells composed of fused spicules of the early Cambrian age (Bengtson, 1992) support an argument of fusion of individual skeletal elements to form sclerites, plates, or shells.

Jacobs et al. (2000):

> Thus, the engrailed data reported here, in combination with previous scenarios for the formation of ectodermal armor and recent fossil discoveries, suggest a singular evolution of invertebrate skeletons near the base of the Cambrian, followed by subsequent loss in several lophotrochozoan and ecdysozoan lineages. ... Such an interpretation, if substantiated, would have important implications for the Cambrian radiation, as it would constrain readily fossilizable exoskeletons to a single lineage, leading to a monophyletic clade of bilaterians. This would lead to a closer association of the bilaterian diversification with the base of the Cambrian. ...



> Onychophorans are thought to be the sister taxon of arthropods and are segmented. However, onychophorans lack *engrailed* expression in their dermis. Instead, expression is observed in the posterior half of the developing limb and in a segmental pattern in the lateral mesoderm. The limb staining suggests shared ancestry of the onychophoran and arthropod limbs. However, given the close relationship of Arthropoda and Onychophora, and their segmented body plans, the lack of segmental ectodermal expression in Onychophora suggests that the ancestral role of *engrailed* was not segmentation; this absence may be a consequence of evolutionary loss of skeletons. Onychophoran dermis lacks a chitinous cuticle; thus Onychophora lack an exoskeleton. Furthermore, Cambrian fossils thought to be stem group onychophorans, such as *Microdictyon*, *Hallucinogenia*, and *Xenusion*, bear skeletal elements above the limb on each segment. Therefore, the absence of *engrailed* transcription in the ectoderm of modern Onychophora could well be a consequence of evolutionary loss of exoskeletal elements coincident with the loss of a component of engrailed expression associated with skeletal boundaries. In addition, the Cambrian *Palaeoscolex*, an ecdysozoan (Conway Morris 1997), bears more extensive ectodermal sclerites than modern pripulids, and *Wiwaxia* and *Halkieria* (Conway Morris & Peel 1995) bear more armor than many modern lophotrochozoa. These observations are consistent with the loss of skeletal elements in a number of lineages since the early Cambrian Period.

CONTINUED ON NEXT PAGE

The Early Cambrian Epochs: 2

The Cambrian "Explosion"

Abstract

This page describes the metazoan (animal) evolutionary phenomenon popularly known as the "Cambrian explosion." The apparent discrepancy between divergence ages implied by genetic calibration techniques and a literal interpretation of the fossil record is discussed.

Keywords: Cambrian, Cambrian biota, Cambrian explosion, Cambrian radiation, fossil record, evolution, Metazoan radiation

"This explosion is perhaps the most striking single event documented by the fossil record. In the strict sense, the explosion refers to a geologically abrupt appearance of fossils representing all except two of the living [animal] phyla that had durable (easily fossilizable) skeletons. One of those two phyla is the Porifera (sponges), which was present in the fossil record at an earlier time. The other is the Bryozoa, a phylum that contains some soft-bodied groups and may well have been present but not yet skeletonized. A number of enigmatic organisms of obscure relationships also appear during the explosion, enriching the early Cambrian fauna. Precision dating indicates that the explosion began at 530 Ma (million years ago) and ended before 520 Ma." Bowring *et al*.

Introduction

The abrupt appearance of a diverse and highly derived fauna in the brief Tommotian and Atdabanian Stages of the Lower Cambrian is widely known as the 'Cambrian Explosion.' Although that particular phrase only came into common usage in the early to mid 1970s, the event itself has long been recognized as a phenomenon demanding some accommodation from evolutionary theory. As early as 1859, Charles Darwin drew attention to the matter in *Origin of Species*, and it is probable he had considered the matter for many years prior to that.

However, despite the rapid proliferation of evolutionary novelties which undoubtedly occurred at this time, at least some of the phenomenon is attributable to the acquisition of preservational characteristics - 'hard parts' - and multiple lines of evidence reveal that life was already highly diversified prior to the Tommotian. The fossil record is continually yielding more and better evidence of pre-Tommotian life, from the earliest biochemicals extracted from ~3,800 Ma cratonic rocks of southwest Greenland, through the perplexing grotesquery of the Ediacarans, to the strangely quiescent Fortunian age, when we find little more than a few small, undistinguished shelly remains.

Despite this, the paleontological evidence does not, generally corroborate molecular clock studies (contrary to the almost bizarre view expressed in Ayala *et al*., 1998). Bruce Runnegar (1982, p. 397) notes: "Few of the known late Precambrian animals have been closely related to Cambrian organisms, and none of the associated or coeval trace fossils has been thought to have been produced by the animals observed more directly. � What the trace fossil record does tell us, is that there were few large, mobile, bottom-dwelling animals before the end of the [Ediacaran]."

[Also see Xiao & Knoll 2000, top of p. 785a.]

The Tommotian and Atdabanian Ages (530 to 519 Ma)

The oldest known shelly fossils, simple tubes of the family Cloudinidae, first appear very near the end of the Proterozoic. Shelly fossils become more common and more diverse in the basal Cambrian �

(1993).

Related Topics

Further Reading

- Wonderful Life � Stephen J. Gould. Gould (1989).
- The Crucible of Creation � Simon Conway Morris. Conway Morris (1998).

Related Pages

- Ediacaran-Lower Cambrian Column
- Ediacaran Biota
- Cambrian Period
- Replaying Gould: A critical review of some of the arguments presented in his book *Wonderful Life*.

Other Web Sites

- Knoll & Carroll 1999
- University of Bristol page

The "Small Shelly Fauna"

"Small shelly fossils near the base of the Cambrian mark the transition to a skeletonized fauna and the metazoan-dominated Phanerozoic fossil record. The recovery of articulated specimens composed of multiple sclerites discussed above, such as Wiwaxia, *Halkieria* and *Microdictyon*, suggests that much of comprising the so-called �small shelly fauna� � but this radiation is modest compared to the explosive diversification of the late Early Cambrian, a phenomenon which has come to be known as the Cambrian Explosion.

For a very long time, non-shelly fossils were unknown or poorly understood, the metazoan status of the Ediacarans was famously a matter of debate, and other lines of evidence had yet to be discovered. Thus, as far as anybody could be sure, the shelly fossil record was a literal record of metazoan evolution, and it seemed to be telling us that in the late Early Cambrian animals diversified explosively from almost nothing to approximately the full range of basic archetypes known today, in as little as 10 million years.

However, "[t]he presence of true, though soft-bodied, triploblasts is now documented by worm burrows, by radular markings and body impressions of early mollusks, and by phosphatised embryos, of Ediacaran age." Seilacher *et al*. (1998: 80). Some, such as *Kimberella* and *Parvancorina*, can even be tentatively assigned to extant phyla. Nevertheless, although recent discoveries have greatly extended the record of sponges and bilateral animals, the earliest unequivocal paleontological evidence of metazoan life is no more than 600 Ma. Bromham *et al*. 1998).

the remaining "small shelly fauna" represent elements similarly employed as ectodermal armor in bilaterian Metazoa that have yet to be recovered in an articulated form. In addition, recent finds of cap-shaped shells composed of fused spicules of the early Cambrian age (Bengtson, 1992) support an argument of fusion of individual skeletal elements to form sclerites, plates, or shells (Haas, 1981).

"Thus, the engrailed data reported here, in combination with previous scenarios for the formation of ectodermal armor and recent fossil discoveries, suggest a singular evolution of invertebrate skeletons near the base of the Cambrian, followed by subsequent loss in several lophotrochozoan and ecdysozoan lineages. Such an interpretation, if substantiated, would have important implications for the Cambrian radiation, as it would constrain readily fossilizable exoskeletons to a single lineage, leading to a monophyletic clade of bilaterians. This would lead to a closer association of the bilaterian diversification with the base of the Cambrian." Jacobs *et al*. (2000: 345).

Phosphatized Embryos

Reports of fossilized eggs and other early developmental stages of marine invertebrates are rare, probably mostly due to the difficulties of recognizing them. However, there is an abundance of small globular structures in the fossil record, leading up to and including that of the Cambrian.

- Zhang and Pratt 1994 reported Middle Cambrian spherical fossils, 0.3 mm in diameter, that under a smooth membrane preserved a polygonal pattern which the authors interpreted as remains of blastomeres belonging to 64- and 128-cell stages of arthropod embryos. In some other cases, at least a general resemblance to eggs has been noted.
- Bengtson & Zhao (1997) report two

such occurrences of globular fossils from basal Cambrian rocks are eggs containing identifiable embryos of metazoans.

(A)  (B)

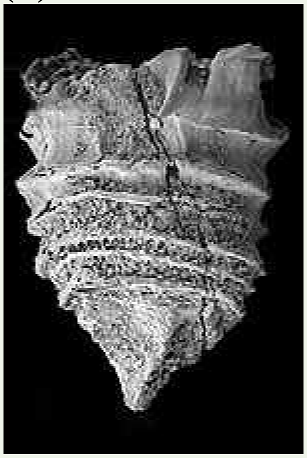


Fig. 1: (A) Reproduction of fig. 1A from Bengtson & Zhao (1997), a SEM image depicting a suggested metazoan embryo – possibly *Olivooides multisulcatus* – at approximately the 256-cell stage. Sample is NGMC (National Geological Museum of China) 9351 from the basal Cambrian Dengying Formation exposed in the Shizhonggou section, Shaanxi Province, China; scale is 500�m.

(B) Reproduction of fig. 1K from Bengtson & Zhao (1997), a SEM image of *Olivooides multisulcatus*. Sample is CAGS (Chinese Academy of Geological Sciences) 32372, also from the Dengying Formation exposed in the Shizhonggou section; scale is the same as A.

Whereas a literal interpretation of the Cambrian fossil record requires the near-simultaneous, �late arrival� of nearly all metazoan phyla, recent genetic evidence reveals a different pattern, sometimes known as the �slow burn� or �early arrival� hypothesis. Age estimates derived from calibrated gene divergence studies tend to vary considerably today � the science is new � but a consistent pattern emerges, nevertheless. These studies all conclude that the major animal groups became separated from one another hundreds of millions of years before the

Wray *et al*. (1996)

Genetic evidence has been used to suggest significant metazoan diversity far pre-dating the Ediacaran fossils (*e.g*. Wray *et al*., 1996: "Calibrated rates of molecular sequence divergence were used to test this hypothesis. Seven independent data sets suggest that invertebrates diverged from chordates about a billion years ago, about twice as long ago as the Cambrian.

Cambrian. Some studies (*e.g*. the classic Wray *et al*., 1996) place the age of the primary division of animals into protostomes and deuterostomes at around 1,200 Ma � much more than twice the age of the Cambrian Explosion.

Protostomes apparently diverged from chordates well before echinoderms, which suggests a prolonged radiation of animal phyla.")

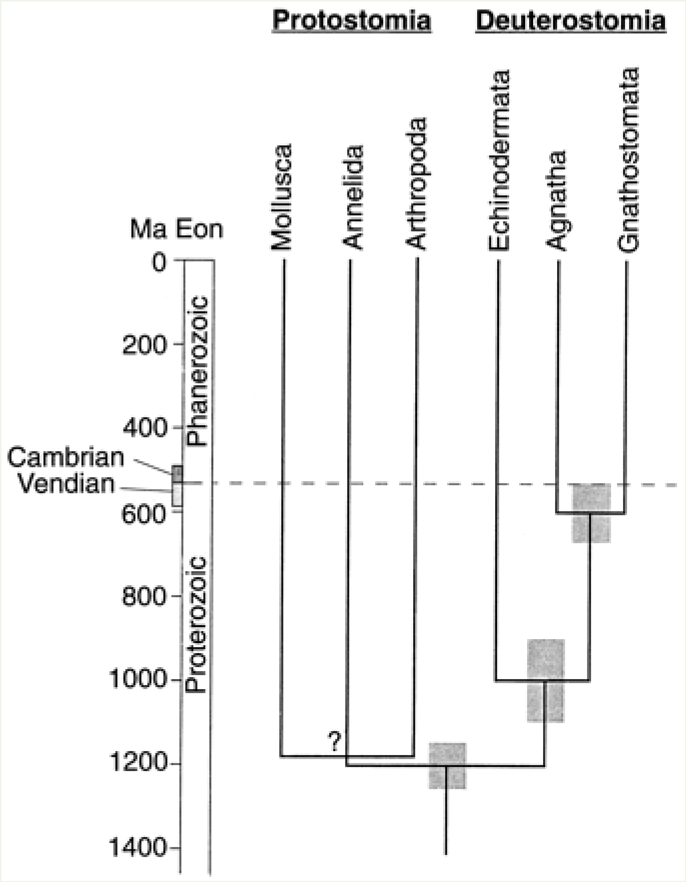
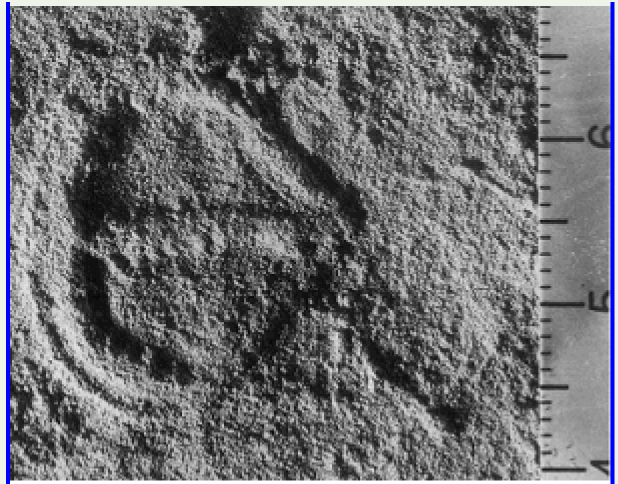


Fig. 1: Reproduction of fig. 2 from Wray *et al.* 1996 showing their estimated divergence times for selected metazoan phyla, based on seven genes, with standard errors indicated by shaded bars. The three estimated divergence times nest in agreement with well-corroborated phylogenetic relationships. Note that the chordate-echinoderm and chordate-protostome divergence times are significantly different from each other. Divergence times among the three protostome phyla were not estimated in their analysis. Although Wray *et al.* 1996 considers "the trend of the data to be more compelling than the exact numerical estimates" of divergence dates, the authors regard their conclusions as "incompatible with the Cambrian explosion hypothesis...."

The Cambrian Explosion documents a real and dramatic radiation of skeletal morphologies, which might represent the parallel uptake of skeletonisation by numerous pre-existing, soft-bodied lineages or, alternatively, a rapid diversification within a relatively few already-skeletonized lineages. The resulting morphological disparity � as measured by the number of major animal types � was at least as great as the present. "Analysis of animal skeletons in relation to the multivariate, theoretical �Skeleton

Space� has shown that a large proportion of these options are used in each phylum. [The] structural elements deployed in the skeletons of Burgess Shale animals (Middle Cambrian) incorporate 146 of 182 character pairs defined in this morphospace. Within 15 million years of the appearance of crown groups of phyla with substantial hard parts, at least 80 percent of skeletal design elements recognized among living and extinct marine metazoans were exploited." Thomas *et al*. (2000: 1239). However, the species diversity produced by the Cambrian radiation, judged at the familial and generic levels, was much below that of succeeding periods (there are more than four times as many marine families today).



Parvancorina, a possible arthropod

"*Parvancorina minchami* can be considered a good candidate in support of the notion that arthropods were present in the Ediacaran. *Parvancorina* appears to have had a tall, three-dimentional shape which has been flattened by subsequent compaction. The central axial ridge and the strongly arched anterior 'lobes' may be analogous to the midgut and gastric diverticulae which occur in the Burgess Shale arthropod *Bugressia*. About ten limbs appear to have been present, which may have been biramous. Scale bar in cms.

From **Chris Nedin's Page**

"The Early Cambrian metazoan radiation was accompanied by a marked diversification of organic-walled microorganisms. Early Cambrian protists include prasinophyte and dasyclad green algae, benthic foraminifers, and a diversity of acritarchs. Prokaryotes are represented by the carbonaceous and calcified remains of cyanobacteria, as well as by biogeochemical signatures, both isotopic and molecular." Knoll (1996: 51).

Globosphaeridium, an acritarch, about 23 microns in diameter

Duration

"A span of 40 million years embraces the appearance of the first small, simple shells that may have been secreted by metazoans and the subsequent exuberant diversity of Chengjiang and the Burgess Shale. This is not so short a time for an evolutionary �explosion.� However, the proliferation of animals with well-differentiated hard parts characteristic of specific metazoan phyla was largely restricted to the last 15 million years of this interval." Thomas *et al*. (2000:

1239).

The application of absolute dates "to the boundaries of the Stages of the Lower Cambrian remains a difficult stratigraphic problem, but it is likely that the most critical Stages, the Tommotian and Atdabanian, are probably only 8-10 [million years] in duration; over 50 metazoan orders first appear in the [fossil] record during that interval (Valentine *et al*. 1991)." Valentine (1995: 89). As noted above, precision dating has now constrained the major Cambrian radiation to the interval 530 to 520 Ma (Bowring & Erwin 1998).

Genes or Skeletons?

Charles Darwin (1860) recognized that the sudden appearance of a diverse and highly derived fossil fauna in the Cambrian posed a problem for his theory of natural selection, "and may be truly urged as a valid argument against the views here entertained." Two obvious possibilities are that animal life did, indeed, evolve very abruptly about that time, or, alternatively, had existed long before, but that, for whatever reason, we have failed to find fossil evidence: the "late-" and "early-arrival" models, respectively.

The two patterns � Cambrian Explosion versus a very long (though obscure) metazoan history � are not necessarily incompatible, because they are based upon different criteria. The genetic evidence documents lines of descent and inheritance, irrespective of morphology, whereas the fossil record documents only the external expression of the genes.

Late-Arrival Models

The �late arrival� model embodies a literal interpretation of the fossil record: that the evolution of the main animal groups took place both late in Earth�s history, and as we now know, extremely rapidly.

What kind of mechanisms could have prompted such an accelerated pace of evolution? Various proposals have been advanced over the years, including:

- A response to the evolution of Hox genes (Erwin *et al*. 1997).
- A rise in macroscopic predation perhaps leading to an �arms-race� style of evolution (Conway Morris

2000). Note, however, that the specific suggestion by Parker (2003) that such an arms race could have been fuelled by the acquisition of high-resolution vision in one or more groups, seems highly implausible (see the review by Conway Morris for a detailed critique).

- Finally, perhaps we can look to the lifting of some external constraint such as insufficient atmospheric oxygen (Runnegar 1982; Brasier 1998, p. 548; Adouette *et al*. 2000, p. 4455).

Nowhere is the late-arrival model more eloquently discussed than in Stephen Gould�s *Wonderful Life* (Gould, 1989), though nearly everyone would now agree that, in this book, Gould overstated his case by some orders of magnitude.

(Read more.)

Early-Arrival Models

Darwin himself preferred the early-arrival explanation, noting that "before the lowest Silurian [the Cambrian system had not yet been recognized] stratum was deposited, long periods elapsed, as long as, or probably far longer than, the whole interval from the Silurian age to the present day; and that during these vast, yet quite unknown, periods of time, the world swarmed with living creatures." Darwin (1860).

Today we might regard Darwin�s views as wonderfully prescient, for numerous Precambrian fossils have now indeed been collected, and modern techniques � impossible in Darwin�s day � such as �molecular clock� studies, strongly indicate metazoan evolutionary events having occurred deep within the Precambrian.

There can be little doubt, on the basis of trace evidence alone, that bilaterian metazoans existed in the Ediacaran, and possibly early in the Ediacaran. Although some traces are simple, rather featureless, winding trails, "others display transverse rugae and contain pellets that can be interpreted as of fecal origin. The bilaterian nature of these traces is not in dispute. Furthermore, such traces must have been made by worms, some of which had lengths measured in centimetres, with through guts, which were capable of displacing sediment during some form of peristaltic

The Doushantuo Formation

The Doushantuo Formation, exposed near Weng'an in south central China, is of early Ediacaran age; ~590 Ma at its base to ~565 Ma at its top. Soft-tissue fossils preserving cellular structures provide strong evidence for a diverse biota predating by perhaps 5 million years (Ma) the earliest of the 'classical' Ediacaran faunas from Mistaken Point, locomotion, implying a system of body wall muscles antagonized by a hydrostatic skeleton. Such worms are more complex than flatworms, which cannot create such trails and do not leave fecal strings." Valentine (1995: 90).

Newfoundland, and existing a good 40 to 50 million years before the Cambrian explosion. Martin *et al*. (2000).

Earliest reports from the Doushantuo Formation include Xiao *et al*. (1998), which notes: "Embryos preserved in early cleavage stages indicate that the divergence of lineages leading to bilaterians may have occurred well before their macroscopic traces or body fossils appear in the geological record" (p. 553).

The documented biota now includes probable algae, sponges, cnidarians and bilaterians. Unfortunately, diagenetic effects are sometimes difficult to distinguish from genuine biological structures, so we can expect the significance of this evidence to be debated for some time to come yet.

(Read more about the Doushantuo Phosphate.)

Because several instances of this type of preservation have now been found, it may be that metazoan embryos are not uncommon as fossils but have simply been overlooked because of their minute size and nondescript morphology. If this is so it may provide us with the means to obtaining insight into the earliest stages of metazoan evolution; perhaps for establishing better paleontological dates for important divergence dates, and for reconciling genetic and fossil evidence.

"The lack of any evidence of horizontal burrowing in rocks older than about 575 Mya and of vertical burrowing in rocks older than 543 Mya is a strong argument that there existed no animals about 1 cm or longer that were capable of disturbing sedimentary layers before this time. When they do appear, these bilaterian traces indicate the presence of animals that had AP [anterior-posterior] differentiation, but there is no evidence of limbs" (Erwin & Davidson 2002, p. 3023, but note these authors were apparently unaware of *Arenicolites*).

"*Arenicolites* is a simple U-shaped burrow oriented perpendicular to bedding. Different types of *Arencolites* can be interpreted on the basis of the breadth of the U. The generally accepted interpretation for *Arenicolites* is that it was a dwelling burrow."

From **Trace Fossil Image Database**

In preserving evidence of bilaterians, the Ediacaran

Sets of

record provides constraints on the protostome-deuterostome (P-D) divergence. If *Kimberella* is indeed a mollusc, as suggested by Fedonkin & Waggoner 1997, or certain trace fossils recorded from the Ediacara Hills and Zimnie Gory are correctly interpreted as radula scratches, we have evidence for derived protostomes at 555 Ma. Similarly, if *Arkarua adami* (from the Pound Subgroup, South Australia; Gehling 1987) is correctly interpreted as an echinoderm, we have evidence for a derived deuterostome of similar age. In either case, it follows that the protostome-deuterostome split must have occurred well before 555 Ma, which is consistent with most �molecular clock� studies.

paired hypichnial ridges strongly hint at an arthropod *s.l.* presence.

The latter, however, mostly favour a P-D split far deeper in the Precambrian: some as early as 1,200 Ma (table 1). If correct, then the Cambrian explosion is clearly an artifact.

Authority	Eukaryote Divergence	Fungi/Plant+Animal	P-D Divergence
Wray *et al*. (1996)			1,200 Ma
Doolittle *et al.* 1996	~2,000 Ma	965 Ma	670 Ma
Feng *et al.* 1997	2,188 Ma	1,272 Ma	850 Ma
Ayala *et al*. (1998)			670 Ma
Bromham *et al*. (1998)			>680 Ma
Wang *et al.* 1999		1,576 Ma	
Heckman *et al.* 2001		~1,600 Ma	1,000 Ma

Table 1: Divergence dates offered by various authorities.

The nature of the last common P-D ancestor (PDA) is explored in Erwin & Davidson 2002 which concludes that the last PDA must have been an extremely simple organism because there is no fossil trace evidence of complex bilaterians prior to 555 Ma, yet the mollusk interpretation of *Kimberella* requires the PDA to be older than this (though see de Robertis & Sasai 1996 and Holland 2002 for other perspectives).

The usual counter-argument, for a complex PDA, is met with the observation that "[a]lthough the heads, hearts, eyes, etc., of insects, vertebrates and other creatures carry out analogous functions, neither their developmental morphogenesis, nor their functional anatomies are actually very similar if considered in any detail. � [Whereas t]he regulatory processes that underlie development of specialized differentiated cells are indeed very old, conserved, plesiomorphic features. In contrast, the morphogenetic pattern formation programs by which the body parts develop their form are clade-specific within phyla or classes" (Erwin & Davidson 2002, p. 3025)

Not only is a very simple PDA consistent with the increasingly dependable and well-resolved fossil record, taking a developmentally explicit view of evolution, it seems inconceivable that a complex organism could survive the mutation which reversed the polarity of the blastopore. The characters involved in an ontogenetically early development like this, subsequently become so �developmentally networked� (Arthur, 1997, or �generatively entrenched� in the nomenclature of Wimsatt 1986) that the requirement for internal coadaptation �freezes� them in, preventing any viable change. This view is consistent with Nielsen�s observation (2001, p. 85) that the mouth openings of the � Protostomia and Deuterostomia, cannot *a priori* be regarded as homologous."

Nielsen considers that a through-gut was "probably ancestral" (Nielsen 2001, p. 83). Erwin & Davidson 2002 also favour a PDA with a through-gut (p. 3029); I, however, do not.

Driving or Underlying Mechanisms

"Molecular evidence from living organisms indicates that the animal, algal, and fungal kingdoms had a lengthy, but largely invisible, Precambrian history. The abrupt appearance of many different kinds of hard-bodied and soft-bodied fossils at the close of the Precambrian is therefore a result of the rise of large, resistant or mineralized organisms from tiny inconspicuous and insubstantial ones. In making this transition, it seems possible that small but unidirectional environmental changes were amplified by the global biota in an opportunistic fashion." Runnegar (1992: 88-89).

Mechanisms

Questions as to why the radiation occurred precisely when it did, and had the breadth that is observed, are still controversial. Some workers search for an environmental stimulus. At one time it was thought that rising oxygen levels might have triggered the explosion, but recent work suggests that adequate levels were reached much earlier. Knoll (1996). Changes in the chemistry and circulation of the linked atmosphere–ocean system are nevertheless suspected to have played a role. On the other hand, the metazoans must have evolved to the point where the explosion was possible. A sophisticated system of genome regulation capable of reorganizing the pattern-formation genes that mediate the development of diverse body plans was clearly required. Valentine *et al*. (1999).

Several theories have been advanced to explain the Cambrian Explosion:

1. The chemistry of the oceans changed to allow the secretion of mineral shells.
2. An "arms race" developed between predators and prey- the evolution of predators was forcing prey species to evolve protective shells or be weeded out by extinction.
3. The oxygen levels in the atmosphere increased to a point that made energetic, aerobic metabolisms possible for multicellular animals.

"Late Proterozoic carbon isotopic profiles display strong negative as well as positive excursions. Negative excursions are specifically associated with the major ice ages that mark immediately pre-Ediacaran time. Much research is currently focused on this unusual coupling of climate and biogeochemistry, and both paleoceanographic models and clustered phytoplankton extinctions suggest that these ice ages had a severe impact on the biota – potentially applying brakes to early animal evolution." Knoll & Carroll (1999). Perhaps, also, there was an element of "the brakes coming off" after the Varanger-Marinoan Glaciation – the only ice age that has put glaciers at sea level in equatorial latitudes.

Positive $d^{13}C$ excursions are sometimes interpreted as records of increased organic (biological) productivity.

"These events also overlap the first global episode of sedimentary phosphate deposition, and they occur at a time when the amount of oxygen in the atmosphere and hydrosphere may have increased significantly. They also coincide with a possible secular change in the mineralogy of non-skeletal, sedimentary carbonates, and with the breakup of a long-lived and largely low-latitude supercontinent." Runnegar (1992: 88).

Why No New Baupl�ne After the Cambrian?

Knoll (2003) favours an ecological explanation: "as the world filled ecologically, evolutionary opportunities for further new body plans dwindled" (p. 223).

I don�t find this explanation totally satisfying. Rather, I think it is only a partial explanation, adequate to account for the failure of new multicellular organisms to arise *de novo* from unicellular ancestors. But I believe it is internal coadaptation � Arthur�s (1997) �developmental networking� � which prevents complex existing phyla from diverging any further. The necessary early-stage mutations are simply lethal.

Conclusion

The abrupt entry of a diverse and highly derived fauna into the fossil record, during the brief Tommotian and Atdabanian ages of the Early Cambrian, has long been recognized and is now widely known to paleontologists and laymen alike, as the �Cambrian Explosion.� However, despite the rapid proliferation of evolutionary novelties which undoubtedly occurred at this time, at least some of the phenomenon is attributable to the acquisition of preservational characteristics � �hard parts� � and multiple lines of evidence reveal that life was already highly diversified prior to the Tommotian.

It is to be expected that morphologically diversity should lag behind genetic diversity. This is especially true of organisms which are morphologically simple to begin with. Bacteria and Archaea look very much alike and, prior to genetic sequencing, they were classified together even though their genes now tell us they are as different as elephants and pond scum � maybe more so.

This expectation is borne out by the generally much greater ages attributed to the divergences of all megascopic lineages by molecular clock methods than is revealed by the fossil record.

Representatives of different high level taxa diverge from one another very early in ontogeny. It is at least intuitively reasonable that the ancestral organisms which experienced the �homologous� phylogenetic divergences, were very simple. For example, the last common protostome-deuterostome ancestor is unlikely to have been a morphologically complex animal. Moreover, once one of these �early� mutations has occurred, it is soon �frozen� in by subsequent internal coadaptation.

These realizations permit us to reconcile diverse observations, such as:

- The very early evolution of life generally (> 3,500 Ma), and eukaryote life in particular (> 1,200 Ma);

- Molecular and microfossil evidence for an ancient (~ 1,000 Ma) diversification of eukaryotes;

- Our failure to find convincing fossil evidence of advanced, megascopic eukaryotes, especially animals, until after ~600 Ma;

- The *apparently* rapid origin of very many crown group metazoans in the ~35 million year interval from ~565 Ma to ~530 Ma (the misnamed Cambrian Explosion);

- The observation that few fundamentally new metazoan body plans (some would say none) have arisen since.

Links

Rachel Wood **The Ecological Evolution of Reefs** - Annu. Rev. Ecol. Syst. 1998. 29:179�206

Cambrian Stratigraphy

Precambrian to Cambrian - notes

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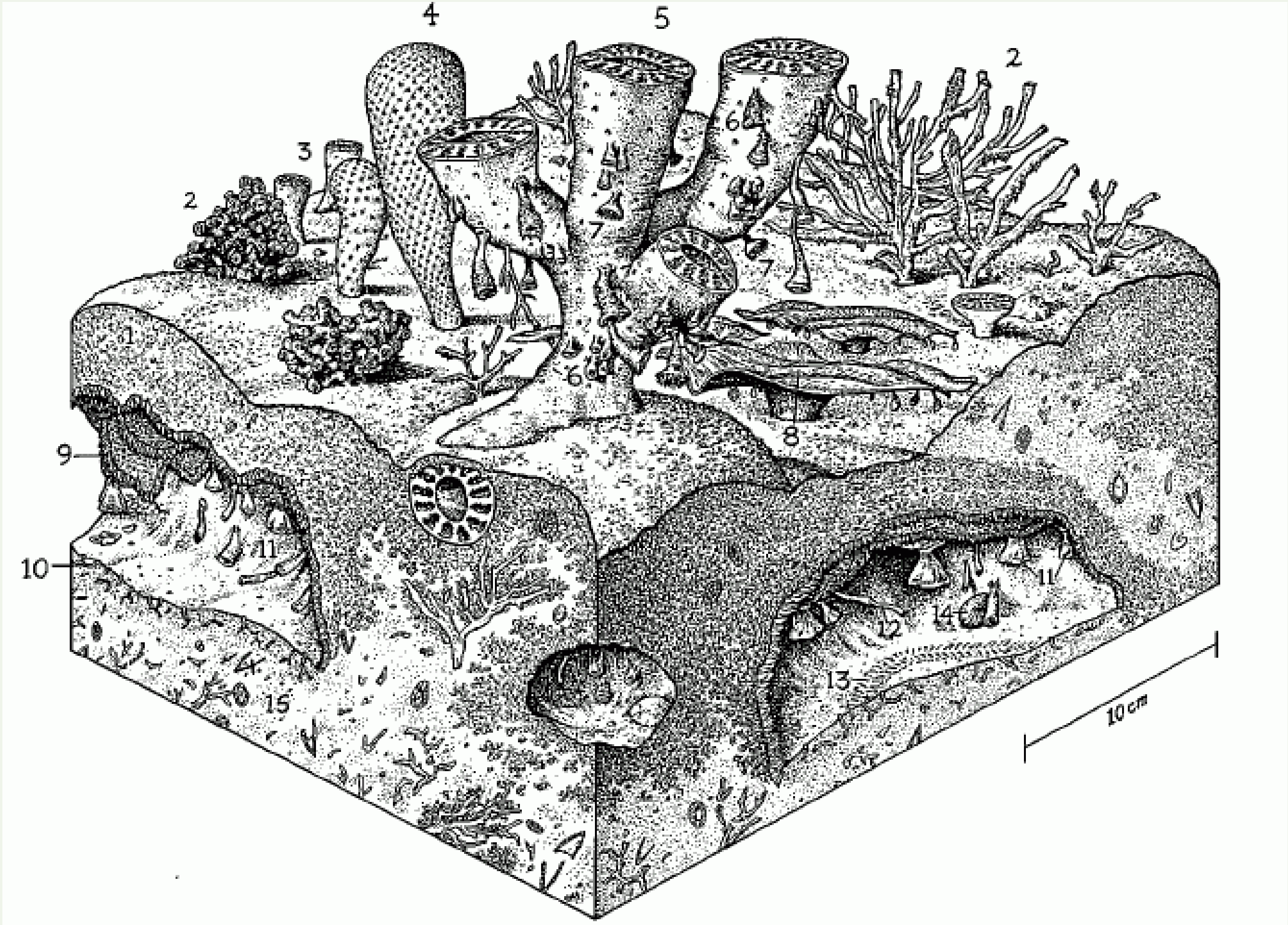
The "Early Cambrian" Epochs:1

The Terreneuvian Epoch and Cambrian Epoch 2: 542 to ~510 million years ago



Reconstruction of an Early Cambrian reef community (from 97). 1. *Renalcis* (calcified cyanobacterium); 2: branching archaeocyath sponges; 3: solitary cup-shaped archaeocyath sponges; 4: chancellorid (?sponge); 5: radiocyath (?sponge); 6: small, solitary archaeocyath sponges; 7: cryptic "coralomorphs"; 8: *Okulitchicyathus* (archaeocyath sponge); 9; early fibrous cement forming within crypts; 10: microburrows (traces of a deposit-feeder) within geopetal sediment; 11: cryptic archaeocyaths and coralomorphs; 12: cryptic cribricyaths (problematic, attached skeletal tubes); 13: trilobite trackway; 14: cement botryoid; 15: sediment with skeletal debris.

Rachel Wood - The Ecological Evolution of Reefs (also R. A. Wood, 1998. Reef Evolution.

Introduction: A Time of Radical Change

We use "Early Cambrian" here in its former sense, to include both the "pre-trilobite Cambrian" (Terreneuvian) and the period which roughly extends from the establishment of trilobites to the collapse of archaeocyaths (Cambrian Epoch 2).

This was a time of great change across a wide spectrum, from tectonic develoments (largely unknown, but plainly substantial)) through geographical (marine transgressions as the ocean invaded the land creating shallow continental seas that allowed primitive life to flourish), atmospheric, (rising oxygen and falling carbon dioxide levels), biogeochemical (changing ocean chemistry, promoting biomineralization; especially the upwelling of high phosphorous levels (large phosphorite deposits), enabling organisms to develop skeletons of calcium phosphate), and ecological (the appearance of predation and algae grazers, which meant an end of the Ediacaran idyll). This combination of events would seem to have been responsible for the sudden and remarkable and diversification of metazoan life at this time.

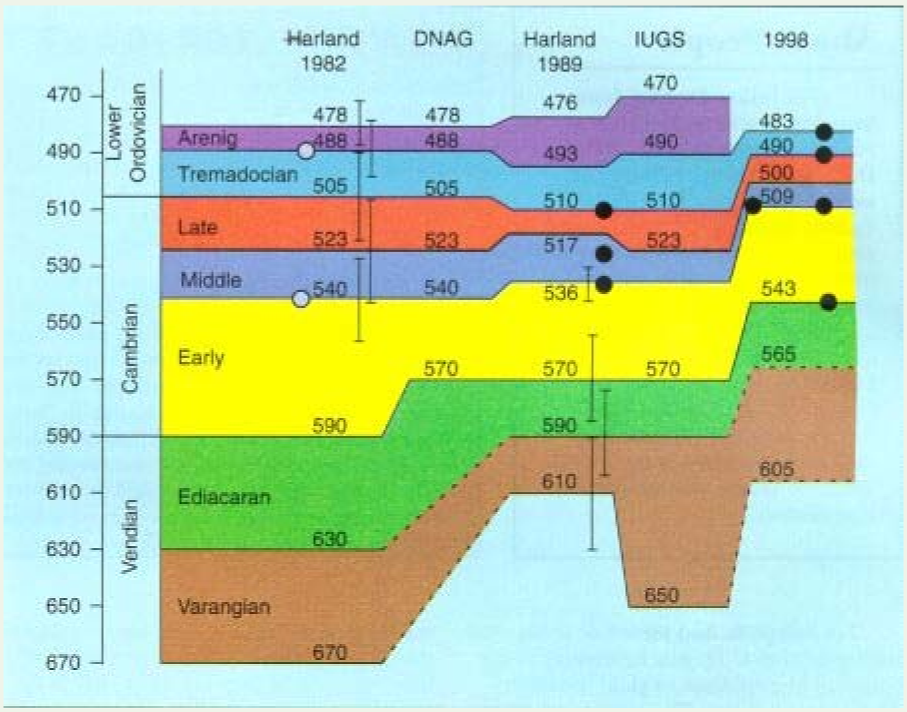
The Early Cambrian was a time of incredible diversification. Quite possibly, this process had begun earlier, but the fossil record first reveals the results during this relatively brief interval of 30 My or so. It seems to have proceeded in three stages, sometimes referred to by the names of three Siberian Cambrian stages: the Manykian, Tommotian and Atdabanian. At the beginning of the epoch, we have simple worm traces, followed shortly by tiny,rather simple shells, the so-called "Small Shelly Fauna" of the earliest Cambrian, or Manykian Age. This was followed by a much more diverse group of shelly animals often referred to as the Tommotian fauna. The relationships of Tommotian animals to living groups are not understood, but it is likely that mollusks also evolved at this time. The Tommotian animals disappeared rather quickly and were followed by the "Cambrian Explosion" of modern groups in the last half of the Early Cambrian (Atdabanian Age). By the end of the Early Cambrian, almost all of the modern phyla had evolved: mollusks, annelid worms, arthropods (including the trilobites), echinoderms, and chordates, to name but a few.

Thus, in the space of about 17 My, roughly from 530 to 513 Mya, the pattern was set for almost all subsequent macroscopic animal life. Many writers have marveled at the amount of new diversity. Stephen Gould�s popular book on the Burgess Shale, of the Canadian Middle Cambrian, **Wonderful Life**, celebrates this explosion in some detail. Gould (1989). What we are now learning is even more startling -- the extraordinary *durability* of this new diversity. Since this was the first radiation of metazoans, its not really surprising that this new life form, expanding into an ecological vacuum, should produce many new varieties. What is a bit harder to explain is why so many of these animals reflect groups which survived for hundreds of millions of years. Most explosive radiations seem to generate a lot more in the way of unsuccessful early models. Perhaps these forms were weeded out in the Manykian and Tommotion Ages. Then again, perhaps we just haven�t found enough fossils yet. The remarkable fossils of Chenjiang, of latest Early Cambrian age, are just now being described in detail. These fossils may eventually give us an entirely new perspective on this key period of early metazoan life.

We do know that the seas rose continuously throughout the Early Cambrian. Higher water is almost always good for life, and this was particularly true during the Paleozoic. Here�s why. The deep oceans are not very useful for life. Plants and photosynthetic bacteria form the base of the foodchain everywhere. Only the top 100 meters or so of the deep oceans are reached by light and can support these organisms. In addition, the deep oceans provide no substrate for plants to attach and get big. However, when the seas rise, they spill over the broad flat coastal plains of the continental shelves. Thus, a small rise in sea level means a lot more area covered by water. This new area of continental sea is shallow -- almost all of it within the "photic zone" in which plants can live. These sunlit continental seas also provide a substrate on which photosynthesizers can attach and grow large. Thus even relatively small increases in sea level can have huge effects on the productivity of the oceans.

Shallow seas also provide a substrate for reef-builders. We tend to think of coral or oyster reefs as picturesque, ecological reservoirs of diversity confined to a relatively small band of tropical waters. But we live in a very unusual corner of Earth history. By comparison with most of the Phanerozoic, our age is bitterly cold and dry. In many, more typical portions of planetary space-time, the shallow seas were almost all warm and dominated by vast reefs which formed complex three-dimensional marine arcologies in wide belts extending for of hundreds, or even thousands of kilometers along the ancient coasts. The Early Cambrian saw the first large reef complexes of this type, although they would be unimpressive by Mesozoic standards. The reef-builders of that epoch were the lacy, vase-shaped archaeocyaths, probably related to sponges, along with other organisms whose affinities are not yet understood.

Age of the Early Cambrian



Age estimates of the Ediacaran, Cambrian, and Early Ordovician
International Subcommision on Cambrian Stratigraphy

Around 1990 it became evident that most of the published radiometric data on the Cambrian were based on Rubidium-Strontium, which gave ages that were up to 50 million years too high. This created a series of drastic revisions, in the age assignment of the Cambrian in general, and especially its lower boundary as shown in the above figure (for more detailed information see Cambrian Stratigraphy) Overall the presumed length of the Cambrian has been reduced from almost 100 million years to little more than half of that. However, it can be seen that the Early Cambrian (yellow band in this diagram) takes the lion's share and in fact remains a longer interval than both the Middle and Late Cambrian combined.

Subdivisions

The Cambrian of the Siberian Platform and adjacent areas are among the best studied Cambrian sequences, and the traditional Siberian Early Cambrian stages (Tommotian, Atdabanian, Botomian, Toyonian) are often used for global comparisons although no formal decision has been made. In in 1992 the Nemakit-Daldynian, now called the Fortunian Stage, was added for the most basal strata, preceeding the Tommotian. The entire series is shown in the table here.

Early Cambrian Life

> During the first 10 million years of the Cambrian Period the Tommotian fauna was replaced by a more diverse biota of larger metazoans participating in more complex communities. The Cambrian fauna was dominated by low-level suspension feeders such as the nonarticulate brachiopods and eocrinoids together with monoplacophoran and hyolith mollusks. Two parazoan groups developed colonial strategies: the archaeocyaths and possibly the sponges. Colonies tend to develop iteratively with new iterative units or modules derived by continuous growth from existing units. The colonial or iterative body plan thus contrasts with the unitary or solitary life mode of most organisms. A number of groups show clear trends towards a greater integration of individuals within the colony and in some cases a differentiation of functions across the colony.

Benchley & Harper (1998).

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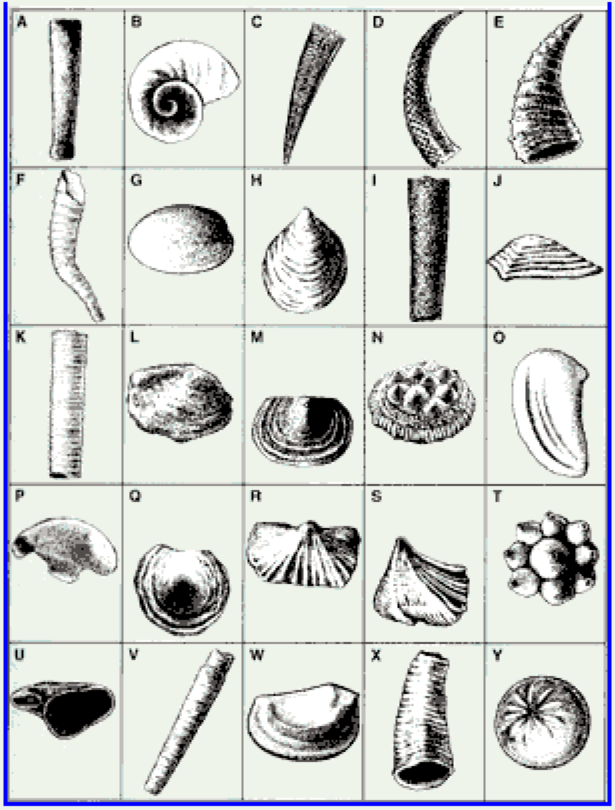
The Small Shelly Fauna

Notes from the literature:

Runnegar (1992):

> [S]tudies of Cambrian fossiliferous strata in Siberia, China, Europe, and Australia have yielded an unexpected range of well-preserved phosphatic microfossils. Most are either tiny shells or the disarticulated components (sclerites) of a protective armour comprised of many parts (Bengtson *et al.*, 1990). These microfossils have become familiar as the "small shelly fossils." Most are original phosphatic skeletons or phosphatic copies of other kinds of hard parts ... .
>
> Stimulated in part by an international endeavour to define the Precambrian-Cambrian boundary for the



global geological time scale, studies of Cambrian fossiliferous strata in Siberia, China, Europe, and Australia have yielded an unexpected range of well-preserved phosphatic microfossils. Most are either tiny shells or the disarticulated components (sclerites) of a protective armour comprised of many parts (Bengtson *et al*., 1990). These microfossils have become familiar as the "small shelly fossils." Most are original phosphatic skeletons or phosphatic copies of other kinds of hard parts ... .

Grotzinger et al. (1998) (abstract):

Abundant calcified fossils occur in the terminal Proterozoic Nama Group, Namibia. The fossils are constrained to occur stratigraphically below the first occurrence of *Phycodes pedum*, overlap in range with known Ediacaran fossil impressions, and extend between ash beds dated at 549 and 543 Ma. At least six distinct morphotypes have been identified to date, suggesting that the proportional representation of calcareous taxa in the terminal Proterozoic fauna was not markedly different from that observed in younger periods. New taxa include branching forms up to 1 cm in diameter that display hexagonal symmetry. This symmetry recalls the tri-radiate geometry of several prominent terminal Proterozoic and basal Cambrian taxa, including *Tribrachidium* and *Anabarites*. Other forms include open cups possibly representative of simple asconoid (vase-shaped) sponges; simple tubes that are functionally (if not necessarily phylogenetically) comparable to sabellid worm tubes, possibly indicating the presence of anterior tentacles or lophophore-like appendages; and more complex multichambered forms. In terms of abundance, the simple cups and tubes are most numerous, followed by the complex branching and multichambered forms, and then the previously described *Cloudina*. All calcified fossils in the Nama appear to represent benthic organisms that lived in close association with thrombolitic and stromatolitic reefs and biostromes, suggesting a strong substrate preference. Generally, they are rare or absent in other facies. Although the forms with hexagonal symmetry may be related to *Anabarites*, most Nama calcareous fossils disappear near the PC-C boundary and do not appear to be closely related to Cambrian small shelly fossils. For the most part, they are as enigmatic as the canonical Ediacaran biota.

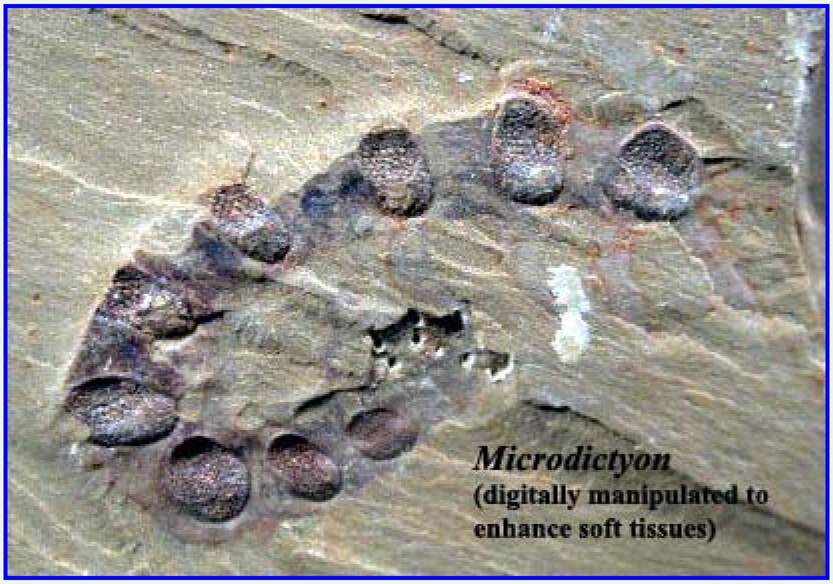
Haas (1981) paraphrase:

Small shelly fossils near the base of the Cambrian mark the transition to a skeletonized fauna and the metazoan-dominated Phanerozoic fossil record. The recovery of articulated specimens composed of multiple

sclerites discussed above, such as *Wiwaxia, Halkieria* and *Microdictyon*, suggests that much of the remaining "small shelly fauna" represent elements similarly employed as ectodermal armor in bilaterian Metazoa that have yet to be recovered in an articulated form. In addition, recent finds of cap-shaped shells composed of fused spicules of the early Cambrian age (Bengtson, 1992) support an argument of fusion of individual skeletal elements to form sclerites, plates, or shells.

Jacobs et al. (2000):

> Thus, the engrailed data reported here, in combination with previous scenarios for the formation of ectodermal armor and recent fossil discoveries, suggest a singular evolution of invertebrate skeletons near the base of the Cambrian, followed by subsequent loss in several lophotrochozoan and ecdysozoan lineages. ... Such an interpretation, if substantiated, would have important implications for the Cambrian radiation, as it would constrain readily fossilizable exoskeletons to a single lineage, leading to a monophyletic clade of bilaterians. This would lead to a closer association of the bilaterian diversification with the base of the Cambrian. ...



> Onychophorans are thought to be the sister taxon of arthropods and are segmented. However, onychophorans lack *engrailed* expression in their dermis. Instead, expression is observed in the posterior half of the developing limb and in a segmental pattern in the lateral mesoderm. The limb staining suggests shared ancestry of the onychophoran and arthropod limbs. However, given the close relationship of Arthropoda and Onychophora, and their segmented body plans, the lack of segmental ectodermal expression in Onychophora suggests that the ancestral role of *engrailed* was not segmentation; this absence may be a consequence of evolutionary loss of skeletons. Onychophoran dermis lacks a chitinous cuticle; thus Onychophora lack an exoskeleton. Furthermore, Cambrian fossils thought to be stem group onychophorans, such as *Microdictyon*, *Hallucinogenia*, and *Xenusion*, bear skeletal elements above the limb on each segment. Therefore, the absence of *engrailed* transcription in the ectoderm of modern Onychophora could well be a consequence of evolutionary loss of exoskeletal elements coincident with the loss of a component of engrailed expression associated with skeletal boundaries. In addition, the Cambrian *Palaeoscolex*, an ecdysozoan (Conway Morris 1997), bears more extensive ectodermal sclerites than modern pripulids, and *Wiwaxia* and *Halkieria* (Conway Morris & Peel 1995) bear more armor than many modern lophotrochozoa. These observations are consistent with the loss of skeletal elements in a number of lineages since the early Cambrian Period.

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The Early Cambrian Epochs: 2

The Cambrian "Explosion"

Abstract

This page describes the metazoan (animal) evolutionary phenomenon popularly known as the "Cambrian explosion." The apparent discrepancy between divergence ages implied by genetic calibration techniques and a literal interpretation of the fossil record is discussed.

Keywords: Cambrian, Cambrian biota, Cambrian explosion, Cambrian radiation, fossil record, evolution, Metazoan radiation

"This explosion is perhaps the most striking single event documented by the fossil record. In the strict sense, the explosion refers to a geologically abrupt appearance of fossils representing all except two of the living [animal] phyla that had durable (easily fossilizable) skeletons. One of those two phyla is the Porifera (sponges), which was present in the fossil record at an earlier time. The other is the Bryozoa, a phylum that contains some soft-bodied groups and may well have been present but not yet skeletonized. A number of enigmatic organisms of obscure relationships also appear during the explosion, enriching the early Cambrian fauna. Precision dating indicates that the explosion began at 530 Ma (million years ago) and ended before 520 Ma." Bowring *et al.*

Introduction

The abrupt appearance of a diverse and highly derived fauna in the brief Tommotian and Atdabanian Ages of the Terreneuvian and Cambrian Epoch 2 (respectively) is widely known as the 'Cambrian Explosion.' Although that particular phrase only came into common usage in the early to mid 1970s, the event itself has long been recognized as a phenomenon demanding some accommodation from evolutionary theory. As early as 1859, Charles Darwin drew attention to the matter in *Origin of Species*, and it is probable he had considered the matter for many years prior to that.

However, despite the rapid proliferation of evolutionary novelties which undoubtedly occurred at this time, at least some of the phenomenon is attributable to the acquisition of preservational characteristics - 'hard parts' - and multiple lines of evidence reveal that life was already highly diversified prior to the Tommotian. The fossil record is continually yielding more and better evidence of pre-Tommotian life, from the earliest biochemicals extracted from ~3,800 Ma cratonic rocks of southwest Greenland, through the perplexing grotesquery of the Ediacarans, to the strangely quiescent Fortunian age, when we find little more than a few small, undistinguished shelly remains.

Despite this, the paleontological evidence does not, generally corroborate molecular clock studies (contrary to the almost bizarre view expressed in Ayala *et al*., 1998). Bruce Runnegar (1982, p. 397) notes: "Few of the known late Precambrian animals have been closely related to Cambrian organisms, and none of the associated or coeval trace fossils has been thought to have been produced by the animals observed more directly. � What the trace fossil record does tell us, is that there were few large, mobile, bottom-dwelling animals before the end of the [Ediacaran]."

[Also see Xiao & Knoll 2000, top of p. 785a.]

The Tommotian and Atdabanian Ages (530 to 519 Ma)

The oldest known shelly fossils, simple tubes of the family Cloudinidae, first appear very near the end of the Proterozoic. Shelly fossils become more common and more diverse in the basal Cambrian �

(1993).

Related Topics

Further Reading

- Wonderful Life � Stephen J. Gould. Gould (1989).
- The Crucible of Creation � Simon Conway Morris. Conway Morris (1998).

Related Pages

- Ediacaran-Lower Cambrian Column
- Ediacaran Biota
- Cambrian Period
- Replaying Gould: A critical review of some of the arguments presented in his book *Wonderful Life*.

Other Web Sites

- Knoll & Carroll 1999
- University of Bristol page

The "Small Shelly Fauna"

"Small shelly fossils near the base of the Cambrian mark the transition to a skeletonized fauna and the metazoan-dominated Phanerozoic fossil record. The recovery of articulated specimens composed of multiple sclerites discussed above, such as Wiwaxia, *Halkieria* and *Microdictyon*, suggests that much of comprising the so-called �small shelly fauna� � but this radiation is modest compared to the explosive diversification of Cambrian Epoch 2, a phenomenon which has come to be known as the Cambrian Explosion.

For a very long time, non-shelly fossils were unknown or poorly understood, the metazoan status of the Ediacarans was famously a matter of debate, and other lines of evidence had yet to be discovered. Thus, as far as anybody could be sure, the shelly fossil record was a literal record of metazoan evolution, and it seemed to be telling us that in Cambrian Epoch 2, animals diversified explosively from almost nothing to approximately the full range of basic archetypes known today, in as little as 10 million years.

However, "[t]he presence of true, though soft-bodied, triploblasts is now documented by worm burrows, by radular markings and body impressions of early mollusks, and by phosphatised embryos, of Ediacaran age." Seilacher *et al*. (1998: 80). Some, such as *Kimberella* and *Parvancorina*, can even be tentatively assigned to extant phyla. Nevertheless, although recent discoveries have greatly extended the record of sponges and bilateral animals, the earliest unequivocal paleontological evidence of metazoan life is no more than 600 Ma. Bromham *et al*. 1998).

the remaining "small shelly fauna" represent elements similarly employed as ectodermal armor in bilaterian Metazoa that have yet to be recovered in an articulated form. In addition, recent finds of cap-shaped shells composed of fused spicules of the early Cambrian age (Bengtson, 1992) support an argument of fusion of individual skeletal elements to form sclerites, plates, or shells (Haas, 1981).

"Thus, the engrailed data reported here, in combination with previous scenarios for the formation of ectodermal armor and recent fossil discoveries, suggest a singular evolution of invertebrate skeletons near the base of the Cambrian, followed by subsequent loss in several lophotrochozoan and ecdysozoan lineages. Such an interpretation, if substantiated, would have important implications for the Cambrian radiation, as it would constrain readily fossilizable exoskeletons to a single lineage, leading to a monophyletic clade of bilaterians. This would lead to a closer association of the bilaterian diversification with the base of the Cambrian." Jacobs *et al*. (2000: 345).

Phosphatized Embryos

Reports of fossilized eggs and other early developmental stages of marine invertebrates are rare, probably mostly due to the difficulties of recognizing them. However, there is an abundance of small globular structures in the fossil record, leading up to and including that of the Cambrian.

- Zhang and Pratt 1994 reported Middle Cambrian spherical fossils, 0.3 mm in diameter, that under a smooth membrane preserved a polygonal pattern which the authors interpreted as remains of blastomeres belonging to 64- and 128-cell stages of arthropod embryos. In some other cases, at least a general resemblance to eggs has been noted.
- Bengtson & Zhao (1997) report two

such occurrences of globular fossils from basal Cambrian rocks are eggs containing identifiable embryos of metazoans.

(A)  (B)

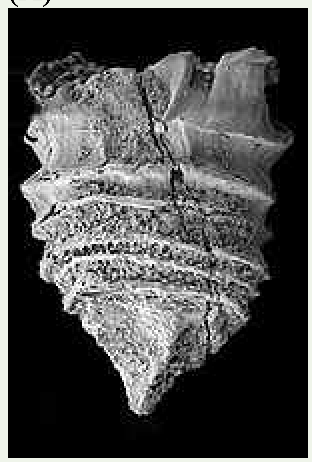


Fig. 1: (A) Reproduction of fig. 1A from Bengtson & Zhao (1997), a SEM image depicting a suggested metazoan embryo – possibly *Olivooides multisulcatus* – at approximately the 256-cell stage. Sample is NGMC (National Geological Museum of China) 9351 from the basal Cambrian Dengying Formation exposed in the Shizhonggou section, Shaanxi Province, China; scale is 500�m.

(B) Reproduction of fig. 1K from Bengtson & Zhao (1997), a SEM image of *Olivooides multisulcatus*. Sample is CAGS (Chinese Academy of Geological Sciences) 32372, also from the Dengying Formation exposed in the Shizhonggou section; scale is the same as A.

Whereas a literal interpretation of the Cambrian fossil record requires the near-simultaneous, �late arrival� of nearly all metazoan phyla, recent genetic evidence reveals a different pattern, sometimes known as the �slow burn� or �early arrival� hypothesis. Age estimates derived from calibrated gene divergence studies tend to vary considerably today � the science is new � but a consistent pattern emerges, nevertheless. These studies all conclude that the major animal groups became separated from one another hundreds of millions of years before the

Wray *et al*. (1996)

Genetic evidence has been used to suggest significant metazoan diversity far pre-dating the Ediacaran fossils (*e.g*. Wray *et al*., 1996: "Calibrated rates of molecular sequence divergence were used to test this hypothesis. Seven independent data sets suggest that invertebrates diverged from chordates about a billion years ago, about twice as long ago as the Cambrian.

Cambrian. Some studies (*e.g*. the classic Wray *et al*., 1996) place the age of the primary division of animals into protostomes and deuterostomes at around 1,200 Ma � much more than twice the age of the Cambrian Explosion.

The Cambrian Explosion documents a real and dramatic radiation of skeletal morphologies, which might represent the parallel uptake of skeletonisation by numerous pre-existing, soft-bodied lineages or, alternatively, a rapid diversification within a relatively few already-skeletonized lineages. The resulting morphological disparity � as measured by the number of major animal types � was at least as great as the present. "Analysis of animal skeletons in relation to the multivariate, theoretical �Skeleton

Protostomes apparently diverged from chordates well before echinoderms, which suggests a prolonged radiation of animal phyla.")

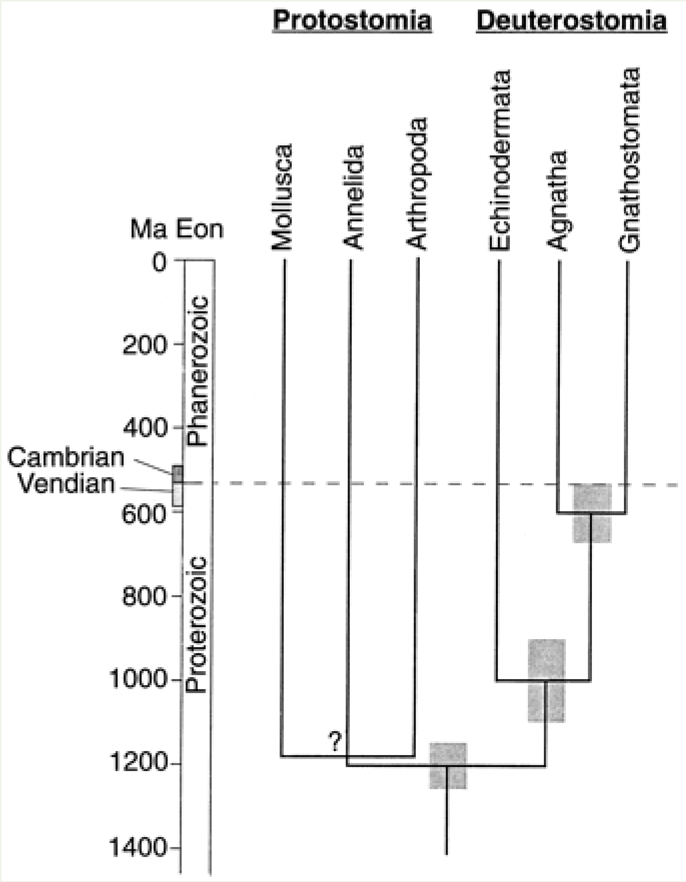
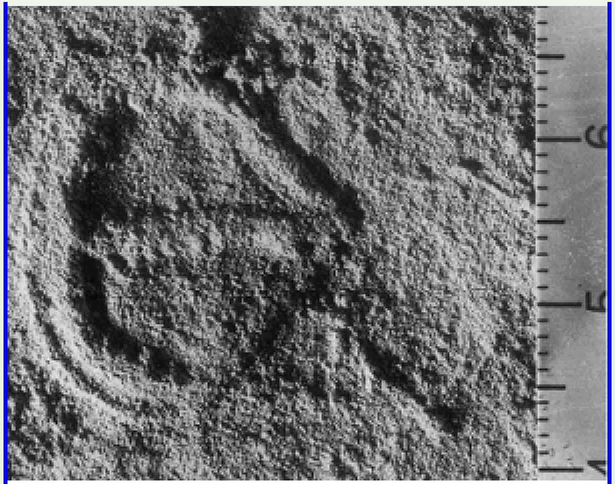


Fig. 1: Reproduction of fig. 2 from Wray *et al.* 1996 showing their estimated divergence times for selected metazoan phyla, based on seven genes, with standard errors indicated by shaded bars. The three estimated divergence times nest in agreement with well-corroborated phylogenetic relationships. Note that the chordate-echinoderm and chordate-protostome divergence times are significantly different from each other. Divergence times among the three protostome phyla were not estimated in their analysis. Although Wray *et al.* 1996 considers "the trend of the data to be more compelling than the exact numerical estimates" of divergence dates, the authors regard their conclusions as "incompatible with the Cambrian explosion hypothesis...."

Space� has shown that a large proportion of these options are used in each phylum. [The] structural elements deployed in the skeletons of Burgess Shale animals (Middle Cambrian) incorporate 146 of 182 character pairs defined in this morphospace. Within 15 million years of the appearance of crown groups of phyla with substantial hard parts, at least 80 percent of skeletal design elements recognized among living and extinct marine metazoans were exploited." Thomas *et al*. (2000: 1239). However, the species diversity produced by the Cambrian radiation, judged at the familial and generic levels, was much below that of succeeding periods (there are more than four times as many marine families today).



Parvancorina, a possible arthropod

"*Parvancorina minchami* can be considered a good candidate in support of the notion that arthropods were present in the Ediacaran. *Parvancorina* appears to have had a tall, three-dimentional shape which has been flattened by subsequent compaction. The central axial ridge and the strongly arched anterior 'lobes' may be analogous to the midgut and gastric diverticulae which occur in the Burgess Shale arthropod *Bugressia*. About ten limbs appear to have been present, which may have been biramous. Scale bar in cms.

From **Chris Nedin's Page**

"The Early Cambrian metazoan radiation was accompanied by a marked diversification of organic-walled microorganisms. Early Cambrian protists include prasinophyte and dasyclad green algae, benthic foraminifers, and a diversity of acritarchs. Prokaryotes are represented by the carbonaceous and calcified remains of cyanobacteria, as well as by biogeochemical signatures, both isotopic and molecular." Knoll (1996: 51).

Globosphaeridium, an acritarch, about 23 microns in diameter

Duration

"A span of 40 million years embraces the appearance of the first small, simple shells that may have been secreted by metazoans and the subsequent exuberant diversity of Chengjiang and the Burgess Shale. This is not so short a time for an evolutionary �explosion.� However, the proliferation of animals with well-differentiated hard parts characteristic of specific metazoan phyla was largely restricted to the last 15 million years of this interval." Thomas *et al*. (2000:

1239).

The application of absolute dates "to the boundaries of the Stages of the Lower Cambrian remains a difficult stratigraphic problem, but it is likely that the most critical Stages, the Tommotian and Atdabanian, are probably only 8-10 [million years] in duration; over 50 metazoan orders first appear in the [fossil] record during that interval (Valentine *et al*. 1991)." Valentine (1995: 89). As noted above, precision dating has now constrained the major Cambrian radiation to the interval 530 to 520 Ma (Bowring & Erwin 1998).

Genes or Skeletons?

Charles Darwin (1860) recognized that the sudden appearance of a diverse and highly derived fossil fauna in the Cambrian posed a problem for his theory of natural selection, "and may be truly urged as a valid argument against the views here entertained." Two obvious possibilities are that animal life did, indeed, evolve very abruptly about that time, or, alternatively, had existed long before, but that, for whatever reason, we have failed to find fossil evidence: the "late-" and "early-arrival" models, respectively.

The two patterns � Cambrian Explosion versus a very long (though obscure) metazoan history � are not necessarily incompatible, because they are based upon different criteria. The genetic evidence documents lines of descent and inheritance, irrespective of morphology, whereas the fossil record documents only the external expression of the genes.

Late-Arrival Models

The �late arrival� model embodies a literal interpretation of the fossil record: that the evolution of the main animal groups took place both late in Earth�s history, and as we now know, extremely rapidly.

What kind of mechanisms could have prompted such an accelerated pace of evolution? Various proposals have been advanced over the years, including:

- A response to the evolution of Hox genes (Erwin *et al*. 1997).
- A rise in macroscopic predation perhaps leading to an �arms-race� style of evolution (Conway Morris

2000). Note, however, that the specific suggestion by Parker (2003) that such an arms race could have been fuelled by the acquisition of high-resolution vision in one or more groups, seems highly implausible (see the review by Conway Morris for a detailed critique).

- Finally, perhaps we can look to the lifting of some external constraint such as insufficient atmospheric oxygen (Runnegar 1982; Brasier 1998, p. 548; Adouette *et al*. 2000, p. 4455).

Nowhere is the late-arrival model more eloquently discussed than in Stephen Gould�s *Wonderful Life* (Gould, 1989), though nearly everyone would now agree that, in this book, Gould overstated his case by some orders of magnitude.

(Read more.)

Early-Arrival Models

Darwin himself preferred the early-arrival explanation, noting that "before the lowest Silurian [the Cambrian system had not yet been recognized] stratum was deposited, long periods elapsed, as long as, or probably far longer than, the whole interval from the Silurian age to the present day; and that during these vast, yet quite unknown, periods of time, the world swarmed with living creatures." Darwin (1860).

Today we might regard Darwin�s views as wonderfully prescient, for numerous Precambrian fossils have now indeed been collected, and modern techniques � impossible in Darwin�s day � such as �molecular clock� studies, strongly indicate metazoan evolutionary events having occurred deep within the Precambrian.

There can be little doubt, on the basis of trace evidence alone, that bilaterian metazoans existed in the Ediacaran, and possibly early in the Ediacaran. Although some traces are simple, rather featureless, winding trails, "others display transverse rugae and contain pellets that can be interpreted as of fecal origin. The bilaterian nature of these traces is not in dispute. Furthermore, such traces must have been made by worms, some of which had lengths measured in centimetres, with through guts, which were capable of displacing sediment during some form of peristaltic

The Doushantuo Formation

The Doushantuo Formation, exposed near Weng'an in south central China, is of early Ediacaran age; ~590 Ma at its base to ~565 Ma at its top. Soft-tissue fossils preserving cellular structures provide strong evidence for a diverse biota predating by perhaps 5 million years (Ma) the earliest of the 'classical' Ediacaran faunas from Mistaken Point, locomotion, implying a system of body wall muscles antagonized by a hydrostatic skeleton. Such worms are more complex than flatworms, which cannot create such trails and do not leave fecal strings." Valentine (1995: 90).

Newfoundland, and existing a good 40 to 50 million years before the Cambrian explosion. Martin *et al*. (2000).

Earliest reports from the Doushantuo Formation include Xiao *et al*. (1998), which notes: "Embryos preserved in early cleavage stages indicate that the divergence of lineages leading to bilaterians may have occurred well before their macroscopic traces or body fossils appear in the geological record" (p. 553).

The documented biota now includes probable algae, sponges, cnidarians and bilaterians. Unfortunately, diagenetic effects are sometimes difficult to distinguish from genuine biological structures, so we can expect the significance of this evidence to be debated for some time to come yet.

(Read more about the Doushantuo Phosphate.)

Because several instances of this type of preservation have now been found, it may be that metazoan embryos are not uncommon as fossils but have simply been overlooked because of their minute size and nondescript morphology. If this is so it may provide us with the means to obtaining insight into the earliest stages of metazoan evolution; perhaps for establishing better paleontological dates for important divergence dates, and for reconciling genetic and fossil evidence.

"The lack of any evidence of horizontal burrowing in rocks older than about 575 Mya and of vertical burrowing in rocks older than 543 Mya is a strong argument that there existed no animals about 1 cm or longer that were capable of disturbing sedimentary layers before this time. When they do appear, these bilaterian traces indicate the presence of animals that had AP [anterior-posterior] differentiation, but there is no evidence of limbs" (Erwin & Davidson 2002, p. 3023, but note these authors were apparently unaware of *Arenicolites*).

"*Arenicolites* is a simple U-shaped burrow oriented perpendicular to bedding. Different types of *Arencolites* can be interpreted on the basis of the breadth of the U. The generally accepted interpretation for *Arenicolites* is that it was a dwelling burrow."

From **Trace Fossil Image Database**

In preserving evidence of bilaterians, the Ediacaran

Sets of

record provides constraints on the protostome-deuterostome (P-D) divergence. If *Kimberella* is indeed a mollusc, as suggested by Fedonkin & Waggoner 1997, or certain trace fossils recorded from the Ediacara Hills and Zimnie Gory are correctly interpreted as radula scratches, we have evidence for derived protostomes at 555 Ma. Similarly, if *Arkarua adami* (from the Pound Subgroup, South Australia; Gehling 1987) is correctly interpreted as an echinoderm, we have evidence for a derived deuterostome of similar age. In either case, it follows that the protostome-deuterostome split must have occurred well before 555 Ma, which is consistent with most �molecular clock� studies.

paired hypichnial ridges strongly hint at an arthropod *s.l.* presence.

The latter, however, mostly favour a P-D split far deeper in the Precambrian: some as early as 1,200 Ma (table 1). If correct, then the Cambrian explosion is clearly an artifact.

Authority	**Eukaryote Divergence**	**Fungi/Plant+Animal**	**P-D Divergence**
Wray *et al*. (1996)			1,200 Ma
Doolittle *et al.* 1996	~2,000 Ma	965 Ma	670 Ma
Feng *et al.* 1997	2,188 Ma	1,272 Ma	850 Ma
Ayala *et al*. (1998)			670 Ma
Bromham *et al*. (1998)			>680 Ma
Wang *et al.* 1999		1,576 Ma	
Heckman *et al.* 2001		~1,600 Ma	1,000 Ma

Table 1: Divergence dates offered by various authorities.

The nature of the last common P-D ancestor (PDA) is explored in Erwin & Davidson 2002 which concludes that the last PDA must have been an extremely simple organism because there is no fossil trace evidence of complex bilaterians prior to 555 Ma, yet the mollusk interpretation of *Kimberella* requires the PDA to be older than this (though see de Robertis & Sasai 1996 and Holland 2002 for other perspectives).

The usual counter-argument, for a complex PDA, is met with the observation that "[a]lthough the heads, hearts, eyes, etc., of insects, vertebrates and other creatures carry out analogous functions, neither their developmental morphogenesis, nor their functional anatomies are actually very similar if considered in any detail. � [Whereas t]he regulatory processes that underlie development of specialized differentiated cells are indeed very old, conserved, plesiomorphic features. In contrast, the morphogenetic pattern formation programs by which the body parts develop their form are clade-specific within phyla or classes" (Erwin & Davidson 2002, p. 3025)

Not only is a very simple PDA consistent with the increasingly dependable and well-resolved fossil record, taking a developmentally explicit view of evolution, it seems inconceivable that a complex organism could survive the mutation which reversed the polarity of the blastopore. The characters involved in an ontogenetically early development like this, subsequently become so �developmentally networked� (Arthur, 1997, or �generatively entrenched� in the nomenclature of Wimsatt 1986) that the requirement for internal coadaptation �freezes� them in, preventing any viable change. This view is consistent with Nielsen�s observation (2001, p. 85) that the mouth openings of the � Protostomia and Deuterostomia, cannot *a priori* be regarded as homologous."

Nielsen considers that a through-gut was "probably ancestral" (Nielsen 2001, p. 83). Erwin & Davidson 2002 also favour a PDA with a through-gut (p. 3029); I, however, do not.

Driving or Underlying Mechanisms

"Molecular evidence from living organisms indicates that the animal, algal, and fungal kingdoms had a lengthy, but largely invisible, Precambrian history. The abrupt appearance of many different kinds of hard-bodied and soft-bodied fossils at the close of the Precambrian is therefore a result of the rise of large, resistant or mineralized organisms from tiny inconspicuous and insubstantial ones. In making this transition, it seems possible that small but unidirectional environmental changes were amplified by the global biota in an opportunistic fashion." Runnegar (1992: 88-89).

Mechanisms

Questions as to why the radiation occurred precisely when it did, and had the breadth that is observed, are still controversial. Some workers search for an environmental stimulus. At one time it was thought that rising oxygen levels might have triggered the explosion, but recent work suggests that adequate levels were reached much earlier. Knoll (1996). Changes in the chemistry and circulation of the linked atmosphere–ocean system are nevertheless suspected to have played a role. On the other hand, the metazoans must have evolved to the point where the explosion was possible. A sophisticated system of genome regulation capable of reorganizing the pattern-formation genes that mediate the development of diverse body plans was clearly required. Valentine *et al*. (1999).

Several theories have been advanced to explain the Cambrian Explosion:

1. The chemistry of the oceans changed to allow the secretion of mineral shells.
2. An "arms race" developed between predators and prey- the evolution of predators was forcing prey species to evolve protective shells or be weeded out by extinction.
3. The oxygen levels in the atmosphere increased to a point that made energetic, aerobic metabolisms possible for multicellular animals.

"Late Proterozoic carbon isotopic profiles display strong negative as well as positive excursions. Negative excursions are specifically associated with the major ice ages that mark immediately pre-Ediacaran time. Much research is currently focused on this unusual coupling of climate and biogeochemistry, and both paleoceanographic models and clustered phytoplankton extinctions suggest that these ice ages had a severe impact on the biota – potentially applying brakes to early animal evolution." Knoll & Carroll (1999). Perhaps, also, there was an element of "the brakes coming off" after the Varanger-Marinoan Glaciation – the only ice age that has put glaciers at sea level in equatorial latitudes.

Positive $d^{13}C$ excursions are sometimes interpreted as records of increased organic (biological) productivity.

"These events also overlap the first global episode of sedimentary phosphate deposition, and they occur at a time when the amount of oxygen in the atmosphere and hydrosphere may have increased significantly. They also coincide with a possible secular change in the mineralogy of non-skeletal, sedimentary carbonates, and with the breakup of a long-lived and largely low-latitude supercontinent." Runnegar (1992: 88).

Why No New Baupl�ne After the Cambrian?

Knoll (2003) favours an ecological explanation: "as the world filled ecologically, evolutionary opportunities for further new body plans dwindled" (p. 223).

I don�t find this explanation totally satisfying. Rather, I think it is only a partial explanation, adequate to account for the failure of new multicellular organisms to arise *de novo* from unicellular ancestors. But I believe it is internal coadaptation � Arthur�s (1997) �developmental networking� � which prevents complex existing phyla from diverging any further. The necessary early-stage mutations are simply lethal.

Conclusion

The abrupt entry of a diverse and highly derived fauna into the fossil record, during the brief Tommotian and Atdabanian ages of the Early Cambrian, has long been recognized and is now widely known to paleontologists and laymen alike, as the �Cambrian Explosion.� However, despite the rapid proliferation of evolutionary novelties which undoubtedly occurred at this time, at least some of the phenomenon is attributable to the acquisition of preservational characteristics � �hard parts� � and multiple lines of evidence reveal that life was already highly diversified prior to the Tommotian.

It is to be expected that morphologically diversity should lag behind genetic diversity. This is especially true of organisms which are morphologically simple to begin with. Bacteria and Archaea look very much alike and, prior to genetic sequencing, they were classified together even though their genes now tell us they are as different as elephants and pond scum � maybe more so.

This expectation is borne out by the generally much greater ages attributed to the divergences of all megascopic lineages by molecular clock methods than is revealed by the fossil record.

Representatives of different high level taxa diverge from one another very early in ontogeny. It is at least intuitively reasonable that the ancestral organisms which experienced the �homologous� phylogenetic divergences, were very simple. For example, the last common protostome-deuterostome ancestor is unlikely to have been a morphologically complex animal. Moreover, once one of these �early� mutations has occurred, it is soon �frozen� in by subsequent internal coadaptation.

These realizations permit us to reconcile diverse observations, such as:

- The very early evolution of life generally (> 3,500 Ma), and eukaryote life in particular (> 1,200 Ma);

- Molecular and microfossil evidence for an ancient (~ 1,000 Ma) diversification of eukaryotes;

- Our failure to find convincing fossil evidence of advanced, megascopic eukaryotes, especially animals, until after ~600 Ma;

- The *apparently* rapid origin of very many crown group metazoans in the ~35 million year interval from ~565 Ma to ~530 Ma (the misnamed Cambrian Explosion);

- The observation that few fundamentally new metazoan body plans (some would say none) have arisen since.

Links

Rachel Wood **The Ecological Evolution of Reefs** - Annu. Rev. Ecol. Syst. 1998. 29:179�206

Cambrian Stratigraphy

Precambrian to Cambrian - notes

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The Fortunian

The Fortunian Age of the Terreneuvian Epoch: 542 to ~535 million years ago

Also known as the Manykaian or Manikajan (etc.), the Fortunian is the earliest of the five Siberian Early Cambrian ages, and also the most recently recognized. The stage and its equivalents were only added to the Cambrian in 1992.

It is characterized by the first appearance of small shelly faunas (SSFs). The SSFs appear sequentially and diversify slowly, but it is not until the following, Tommotian stage that they really take off. They are the earliest well-known complex three-dimensional trace fossils; mostly small, chitinous, calcareous, and phosphatic elements of problematic affinity. Some of them at least formed part of the armour of larger (more normal sized) invertebrate animals; the so-called "coat of mail" creatures like *Halkeria*

Fig. 1: The horizontal burrow trace fossil, *Trichophycus pedum* defines the lower boundary of the Cambrian in the reference section at Fortune Head, southeastern Newfoundland. [Image courtesy of Dr. Gerd Geyer, Institut f�r Pal�ontologie, Bayerische Julius-Maximilians-Universit�t, W�rzburg, Germany.]

The Fortunian is also represented by the first good infaunal trace fossils. The base of the stage is marked by the FAD (First Appearance Datum) of the of burrowing trace fossil *Trichophycus pedum* (formerly *Phycodes pedum*), shown above. This event is dated radiometrically at about 544 Ma, and is thus older (by about 15 million years or more) than the Tommotian-Atdabanian "Cambrian Explosion" proper.

Cambrian Age II (Tommotian)

The Late Terreneuvian Epoch: ~535 to ~521 million years ago

Introduction

"The wave of discoveries that rewrote the story of the earliest Cambrian began when the former Soviet Union mustered sizable teams of scientists to explore geological resources in Siberia after the end of World War II. There, above thick sequences of Precambrian sedimentary rocks, lie thinner formations of early Cambrian sediments undisturbed by later mountain-building events (unlike the folded Cambrian of Wales). These rocks are beautifully exposed along the Lena and Aldan rivers, as well as in other parts of that vast and sparsely populated region. A team headed by Alexi Rozanov of the Paleontological Institute in Moscow discovered that the oldest limestones of Cambrian age contained a whole assortment of small and unfamiliar skeletons and skeletal components, few bigger than 1/2 in (1 cm) long. These fossils have been wrapped in strings of Latin syllables but have been more plainly baptized in English as the "small shelly fossils" (SSFs for short).

In 1969, a 380-page monograph was published in Russian describing the unknown fossils, and Paleontologists who now knew what to look for began to discover parallel sequences scattered- in sites from Meishucun in southern China, and India to Newfoundland and Nova Scotia, and from Shropshire to southern Australia."

J. John Sepkoski Jr, "Foundations - Life in the Oceans" in *The Book of Life*, ed. by Stephen Jay Gould, 1993, Ebury Hutchison, London, pp.48-49

See also The Tommotian Age at Berkeley UCMP

Global events such as a major rise in the level of marine carbonates and phosphates triggered the sudden appearance of phosphate rich shelly-organisms. - *Carbon Isotope Stratigraphy of the Phosphorite-Bearing Precambrian-Cambrian Transition Series of the Lesser Himalaya (Uttar Pradesh, India)* (no longer available)- "a high reading of negative carbon isotope indicates geological events starting with a preceding oceanic anoxic event (OAE). The re-establishment of a well-mixed oxic Late Proterozoic ocean was apparently coupled to the breakup of the Precambrian megacontinent(s) that consequently generated an array of epicontinental seas and bays, notably in the realm of the newly-formed paleotethys. In the wake of restored marine circulation patterns, these shelf areas were inundated by previously stagnant, phosphate-rich seawater, turning the shelves into regions of high primary productivity" (short but technical paper)

The Tommotian was an important period which saw the rise of diversified metazoans with skeletons. This represented the earliest abundant and diverse small skeletonized assemblage stage stratotype in Siberia, and was characterized by a great diversity of SSFs, the first archaeocyaths, primitive molluscs, and inarticulate brachiopods.

The Small Shelly Fauna (SSFs) consists of various calcareous (also some silica, some calcium phosphate) fossils some 1-3 mm long. They represented a variety of organisms: sponges, mollusks, annelids, lobopods, and other forms that do not seem to belong to any recent phylum.

The archaeocyaths were the main Early Cambrian reef formers. They had a distinctive Cone inside a cone structure and a calcareous skeleton. Most were no more than a few centimeters in height

Stratigraphy

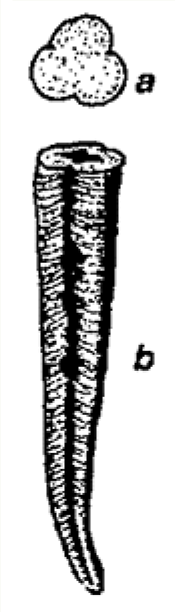
click on subzones to trace the progression of life
earlier<---------------------> later

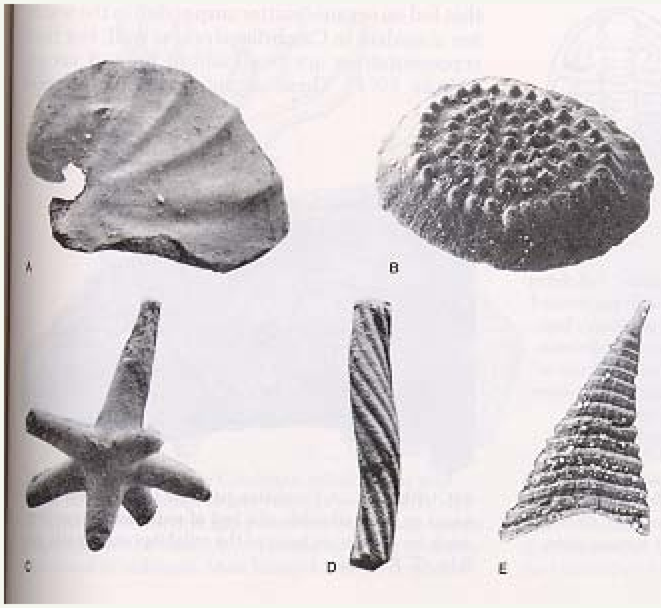
<table>
<tr><td colspan="4">The Tommotian Age
subzones</td></tr>
<tr><td rowspan="2">Aldanocyathus sunnaginicus</td><td colspan="2">Dokidocyathus regularis</td><td rowspan="2">Dokidocyathus lenaicus</td></tr>
<tr><td>Lapworthella tortuosa</td><td>Lapworthella bella</td></tr>
</table>

Marine Invertebrates

Family Anabaritidae
Anabarites trisulcatus (Missarzhevsky)
side view and cross-section
East Yunnan, China
The name *Anabarites* is given to tiny calcium-carbonate tubes, built on a 3-fold symmetry, constructed by creatures of unknown affinity.

Illustration from W.D. Brasier "Towards a biostratigraphy of the earliest skeletal biotas" (p.136, fig.7.8), in J.W. Cowie & M.D. Brasier eds. *The Precambrian-Cambrian Boundary*, Clarendon Press, Oxford, 1989



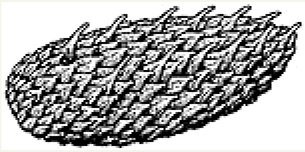


Small Shelly Fauna from the Tommotian Age
From left to right, top to bottom:
Latouchella, a Helcionelloid mollusk; a *Microdictyon*-like form (mineralized part of a lobopod); *Chancelloria* - a spicule from a superficially sponge-like Procoelomate (Class Coeloscleritophora); a vermiform specimen I can't identify (need to look up more references); and *Tommotia*, an angular shell from an animal of uncertain affinities, but presumably another Procoelomate - Class Tommotiida

note: the following passage is from Benchley and Harper, *Palaeoecology*, pp.123-4

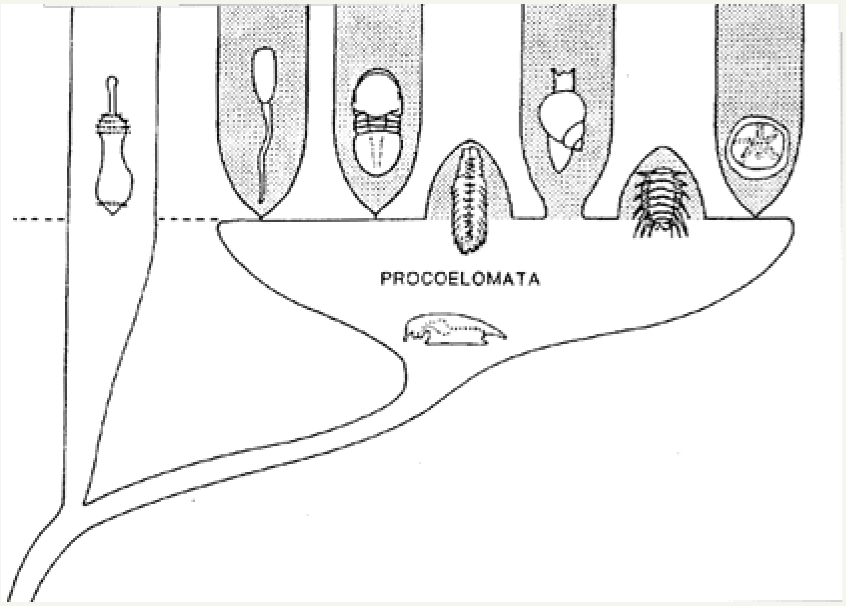
"A distinctive assemblage of small shelly fossils, traditionally labeled the Tommotian fauna. appeared at the Precambrian-Cambrian transition; the assemblage is most extravagantly developed in the lowest Cambrian stage of the Siberian Platform, the Tommotian, which gives its name to the fauna. Much is now known about the stratigraphy and palaeobiogeography of this biota through current interest in the definition of the base of the Cambrian System. Nevertheless the biological affinities of many members of the fauna have yet to be established and, although dominated by minute species, together with small sclerites of larger species, the biota represents the first appearance of diverse skeletal material in the fossil record, some 10 million years before the first trilobites evolved. These faunas also provide opportunities to study the functional morphology of early skeletal metazoans.

This type of fauna is not restricted to the Tommotian Stage; these fossils are also common in the overlying Atdabanian Stage. The less time-specific term, Small Shelly Fauna (SSF) was introduced to describe these assemblages. A variety of phyla united by the minute size of their skeletal components and a sudden appearance at the base of Cambrian are now included in the Tommotian fauna. It probably dominated the earliest Cambrian ecosystems where many metazoan phyla developed their own distinctive characteristics, initially at a very small scale. Soft-bodied organisms had developed some protection against predation and desiccation and support for organs and muscle systems. Functional interpretations are difficult since many of the elements of the fauna are, in fact, sclerites of larger animals such as the halkieriids; moreover, there is still uncertainty regarding the precise identity and affinities of many cap-shaped shells, such as the helcionelloids, in the fauna. Nevertheless some of the mollusk-like shells have been functionally analyzed and suggest that these animals pursued a variety of mobile epifaunal and semi-infaunal life strategies (Peel, 1991); the halkieniids may have constructed U-shaped burrows with their anterior and posterior shells covering the entrance and exit to the burrow system."



Lapworthella, a reconstruction of a Tommotian "coat of mail" Procoelomate animal

"Procoelomates"



The term "procoelomate" was coined by the Swedish paleontologist Jan Bergström to slug-like bilaterian animals that evolved from ancestral aschelminthes (priapulid drawn on the left of the diagram) and gave rise to the various coelomate phyla during the Ediacaran-Cambrian transition. (Lophophorates (Brachiopod), Articulate (Trilobite), Mollusca (gastropod) and Deuterostomia (echinoderm) illustrated). Genetic (RNA) analysis indicates that the various groups of animals based on the coelomate body plan evolved rapidly from this hypothetical "pro-coelomate" ancestor. This agrees with the paleontological evidence of a "Cambrian explosion"

Dr Bergström goes on to suggest that groups of late surviving procoelomates became the strange armoured animals that lived in early Cambrian times. Several of these strange creatures are illustrated here.

Illustration from Jan Bergström, "Metazoan evolution around the Precambrian-Cambrian transition", in *The early evolution of Metazoa and the significance of problematic taxa*, ed. by Alberto M. Simonetta and Simon Conway Morris, Cambridge University Press, p.31 fig.4

Order Mitrosagophora

Family Tommotidae

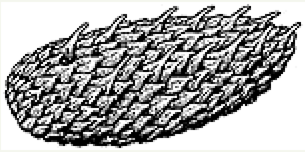
Tommotia species

Four distinct species of Tommotia are known from the Siberian platform, and another from the Baltic.

A related form was *Dailyatia*

illustration from J. John Sepkoski Jr, "Foundations - Life in the Oceans" in *The Book of Life*, ed. by Stephen Jay Gould, 1993, Ebury Hutchison, London, p.50

Order Uncertain

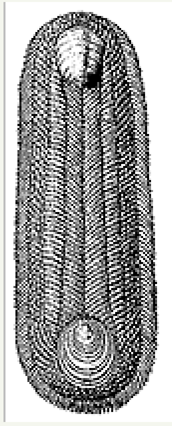


Family Lapworthellidae

Lapworthella tortosa and *L.bella*

Illustration from Mark A.S. McMenamin, "The Emergence of Animals, *Scientific American*, vol. ***, p.87

Order Satchitida / Halkeriida



Family Halkieriidae

Halkeria proboscidea and *Halkeria saciformis*

Siberian Platform.

Length about 3.5 cm

(illustration based on an early Atdabanian specimen from Greenland.)

Halkeria is yet another representative of the "coat of mail" group. Notice the presence of two limpet-shaped shells, which may indicate moluscan affinities. Later forms such as the Middle Cambrian *Wiwaxia* lost the shells and developed long spines instead.

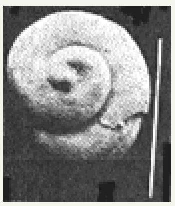
Despite the possession of a shell (or shells), it is not certain that these creatures even are molluscs, although a radula-like structure found in *Wiwaxia* does support molluscan relations. Perhaps they represent a transitional link between the original procoelomates and the Mollusc phylum, or were very primitive molluscs ancestral to all later groups.

lustration from Jerzy Dzik, "Early Metazoan Evolution and the Meaning of It's Fossil Record", in *Evolutionary Biology*, vol. 27, edited by Max K. Hecht *et al*., Plenum Press, New York, fig. 11 p.367

Mollusc-like forms

Phylum, Class and Order uncertain

Family Aldanellidae



Aldanella attleborensis

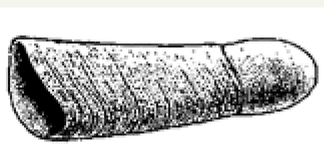
Siberian Platform and Newfoundland

Scale bar 1 mm

These tiny helical, snail-like shells are known only from internal moulds, and constitute an abundant component of the tommotian faunas. They have been traditionally included in the Archaeogastropoda, but appear too early in the fossil record to be gastropods. *Aldanella* has also been placed in the molluscan (Paragastropod) family Pelagiellidae. Distorted and variable growth forms indicate they may not even be molluscs. Even if they are molluscs they probably belong to a distinct extinct class

Phylum Hyolithida

Family Tchuranithecidae



Turcatheca crasseochlia

Siberian Platform

illustration from Jerzy Dzik, "Early Metazoan Evolution and the Meaning of It's Fossil Record", in *Evolutionary Biology*, vol. 27, edited by Max K. Hecht *et al*., Plenum Press, New York, fig. 10 p.365

Phylum Mollusca

Class Helcionoida

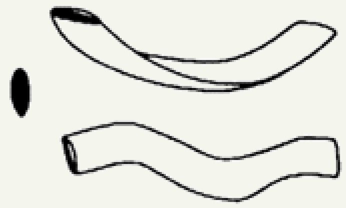
Anabarella sp..

Siberian Platform

Phylum Arthropoda

Class and Order Uncertain

Family Torellellidae

		
Torellella curva Siberian Platform *sunnaginicus* zone	*Torellella lentiformis* Siberian Platform late *sunnaginicus* to *regularis* zone	*Torellella biconvexa* Siberian Platform *lenaicus* zone to early Atdabanian

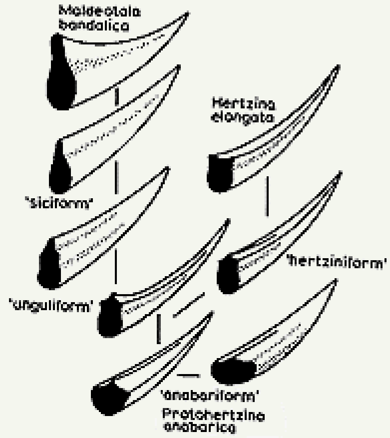
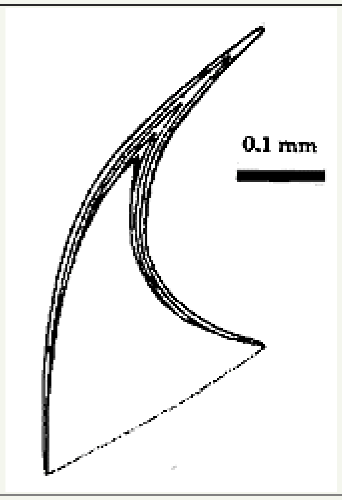
illustrations from W.D. Brasier "Towards a biostratigraphy of the earliest skeletal biotas", in J.W. Cowie & M.D. Brasier eds. *The Precambrian-Cambrian Boundary*, Clarendon Press, Oxford, 1989

Phylum Brachiopoda

Order Paterinida
Aldanotreta
Siberian Platform

Superphylum Deuterostomia

Phylum Protoconodonta *or* Phylum Chaetognatha Class Protoconodonta

Family Protohertzinidae	**Family Fomitchellidae**
	
Protohertzina Siberian Platform and elsewhere illustration from W.D. Brasier "Towards a biostratigraphy of the earliest skeletal biotas", in J.W. Cowie & M.D. Brasier eds. *The Precambrian-Cambrian Boundary*, Clarendon Press, Oxford, 1989	*Fomitchella infundulitiformis* showing growth lines like those found in conodonts. scale bar - 0.1 mm Siberian Platform Illustration from Jerzy Dzik, "Early Metazoan Evolution and the Meaning of It's Fossil Record", in *Evolutionary Biology*, vol. 27, edited by Max K. Hecht *et al.*, Plenum Press, New York, fig. 1 p.342

The earliest metazoan reefs at the base of the Tommotian, as exposed on the Aldan River, Siberia, were already ecologically complex (75). While possessing low diversity, they had erect framework elements of branching archaeocyaths, with a cryptic biota of archaeocyaths and calcified cyanobacteria. These reefs were associated with skeletal debris of a diverse associated fauna; microburrowing deposit-feeders continued to proliferate within the sheltered areas of the framework.

By the middle Tommotian, archaeocyath - cyanobacterial reefs became more diverse and ecologically complex (52) due to the appearance of other sessile, calcified organisms inferred to have been suspension- or filter-feeders. These organisms included radiocyaths, a variety of simple cup-shaped forms known as "coralomorphs," globally rare but locally abundant large skeletal tabulate corals and other cnidarians (53, 78), and stromatoporoid sponges (69). Possible calcarean sponges appeared in the early mid-Tommotian (52); probable sponge borings have been noted within coralomorph skeletons from the Canadian Rocky Mountains (70), and silt-sized microspar grains resembling "chips" from clionid-type sponges have been identified within Lower Cambrian reef cavities (50).

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The Atdabanian

Cambrian Age III: ~521 to ~517 million years ago

Why do We Keep Writing Those Silly Names in Quotation Marks in the Header?

The ICS has not yet tied down all the subdivisions in what used to be the Early Cambrian. Where they don't, we apply the Russian-Kazakhian regional nomenclature. The Atdbanian Age was the third stage of the epoch formerly known as the Early Cambrian. Actually, the ICS doesn't recognize the Early Cambrian, either, and has tentatively divided the first 29 My of the Cambrian into two (one unnamed) epochs, which are each to contain two (likewise unnamed) ages with appropriate (but unspecified) base dates. They will get around to telling us all about it at some (unstated) time in the next year or two -- just as the (unprintable) ICS has been saying for the last ten years. Accordingly, we are somewhat hard put to say what goes where. We*think* the Atdabanian corresponds to Stage 3 because the ICS rashly let slip that Stage 3, like the Atdabanian, should begin with the first appearance of trilobites. But be warned. ICS could decide anything -- or nothing.

During this important age their appeared of macroscopic calcareous (and silica and calcium phosphate) hard parts in many metazoan types, especially the Lophotrochozoa (in brachiopods and mollusks), Ecdysozoa (in arthropods), and Deuterostomia (in echinoderms and vertebrates). As we said, trilobites appeared for the first time, and were to continue to flourish for some hundred million years or more, before going into a slow decline at the end of the Ordovician. Also appearing were Anomalocarids, which became the dominant life form probably until the end Cambrian extinction.

Lobopods

Microdictyon

Microdictyon

Andalusiana sp.
ORDER - Redlichiida
FAMILY - Holmiidae
Lower Cambrian (535 million years old)
Erfoud, Morocco
scale bar in cm
(Paleontological Research Institution)

Links

As always, its useful to check the **Geowhen Database** for the latest from the ICS and for correlation with other systems of chronology. This is particularly true for periods, such as the Cambrian, in which the ICS has not yet completed its work. For a quick orientation, see **The Cambrian Explosion, U of Mn lecture notes**. There are many good links on the Atdabanian Age because many of of the Chenjiang and Sirius Passet fossils are of this age. Many good sites can be found by searching on those names. One of these is an on-line paper by **Zhang *et al*. (2004)**, describing new lophophorates (*Lingulellotreta*) with amazingly detailed preservation from Chenjiang. Earlier work from the same group can be found **here**. The Atdabanian is also the time during which, according to one school of thought, the the rotational axis of the Earth migrated extensively for unknown reasons. A copy of the original eyebrow-raising paper by **Kirschvink *et al*. (1997)** is available. ATW050820.

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The Botomian Age

The Botomian Age of Cambrian Epoch 2: ~517 to ~510 million years ago

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Trilobites and Archaeocyaths diversify

The ICS does not yet recognize any formal divisions of the Early Cambrian. *See* sarcastic comments at Atdabanian Age. We apply the Russian-Kazakhian regional nomenclature. It appears that the Botomian and Toyonian Ages will be combined on that happy day when ICS finally gets around to telling us what to call anything in the first 29 My of the Cambrian.

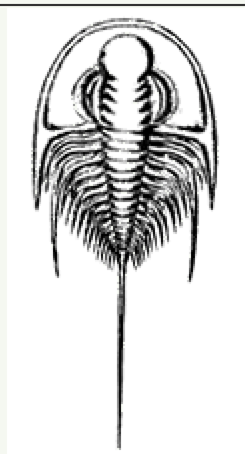
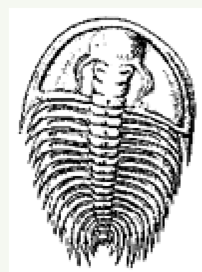
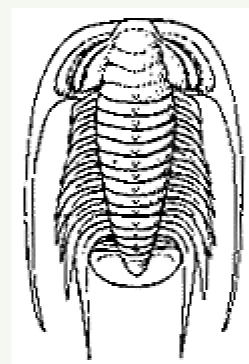
Relative to later ecosystems, the Cambrian ecology was extremely delicate. This may be due to the fact that diveristy was very low, compared to modern ecosystems, and so environmental disruptions could easily wreak havoc (we are witnessing the groundworl of what may well be a similar disaster today - human stupidity and short-sightedness means that large areas of wilderness and biodiversity are being destroyed, to make way for extensive fields of ecologically vulnerable monocultures.)

The Botomian witnessed a mass extinction that may have been even more severe than the end Permian extinction, in terms of absolute percentages of species lost. Some 83% of genera of hard-shelled or -bodied animals did not survive into the Middle Cambrian. However, relative to the rest of the Cambriabn this wasn't so bad. The Cambrian background extinctions between stages was about 40%, compared with about 5% in the Permian. So the Permain extinction was ten times the normal rate whereas the Botomian extinction rate was only twice the background rate.

Bergeroniellus spinosus
Early Cambrian
Lena River, Siberia
(UCMP)

Trilobita

Order **Redlichiida**

Suborder **Olenellina** Family: **Olenellidae** Subfamily: **Olenellinae**	Suborder **Olenellina** Family: **Olenellidae** Subfamily **Waneriinae**	Suborder **Bathynotina** Family: **Bathynotidae**
		
Paedeumias transitans Walcott Parker Slate Vermont, USA length 3 cm (figure from Fenton & Fenton, The Fossil Book, p.218; *see also*: *Treatise on Invertebrate Paleontology*, Vol. O, pp.192-3, Moore, Lalicker & Fischer, *Invertebrate Fossils*, pp.496-7)	*Wanneria walcottana* (Wanner) Pennsylvania, USA length: 6 cm (*Treatise on Invertebrate Paleontology*, Vol. O, p. 197)	*Bathynotus holopyga* (Hall) Vermont, USA length 5 cm (*Treatise on Invertebrate Paleontology*, Vol. O, p. 216)

Stratigraphy

The Toyonian Age subzones		
Bergeroniellus ketemensis	***Lermontovia grandis***	***Anabaraspis splendens***

The Botomian Age subzones

The Middle Cambrian

Cambrian Epoch 3: ~510 to 501 million years ago

Neoproterozoic Era
Tonian Period
Cryogenian Period
Ediacaran Period
Paleozoic Era
Cambrian Period
Terreneuvian Epoch
Cambrian Epoch 2
Middle Cambrian Epoch
Amgan Age
Drumian Age
Guzhangian Age
Furongian Epoch
Ordovician Period
Silurian Period
Devonian Period
Carboniferous Period
Permian Period

Introduction

Something seems to have happened to the oceans at the end of Cambrian Epoch 2. One indicator is that the magnesium content of seawater seems to have dropped. We know this because, in the Early Cambrian, calcium carbonate precipitated out of seawater as aragonite, a the preferred crystal form of calcium carbonate when relatively high concentrations of magnesium are present. When magnesium concentrations in seawater are lower, calcium precipitates as calcite. For reasons we don�t need to get into, both high water and low magnesium are correlated with a higher rate of sea floor spreading -- the creation of new sea bottom from magma which seeps out along mid-ocean fault zones. The Early Cambrian marked a dramatic increase in the rate of sea floor spreading. So, as we have mentioned, the seas rose and magnesium concentrations dropped.

At just about 501 Mya, a crucial threshhold was passed, and the Earth entered a long period of calcite seas. This was to last throughout the remainder of the Early and Middle Paleozoic. At just about this same time, sea levels dropped slightly -- not a great deal, but quite quickly. The combination of physical and chemical changes may have been the cause of the significant faunal turnover we see at that time. The archaeocyaths died out rapidly, quite likely as a result of these changes, and were not replaced by other reef-forming organisms for many millions of years. This caused a further massive physical change in the shallow water environment.

By this time, the metazoan revolution was in full swing. The habitat destruction of the Middle Cambrian may only have selected for even bigger and more mobile forms able to take advantage of the open sea bottom. This was the time of the anomalocarids, Earth�s first really large carnivores, some of whom reached lengths of 2 meters. Andrew Parker has recently emphasized that this was also a time when several key groups evolved eyes. As Parker notes, this has some important correllates. Vision takes much more brainpower than most other senses. Reacting to what one sees also requires quicker and more flexible responses. Further, when hunter and hunted can see each other, both will discover that a higher premium has been placed on mobility.

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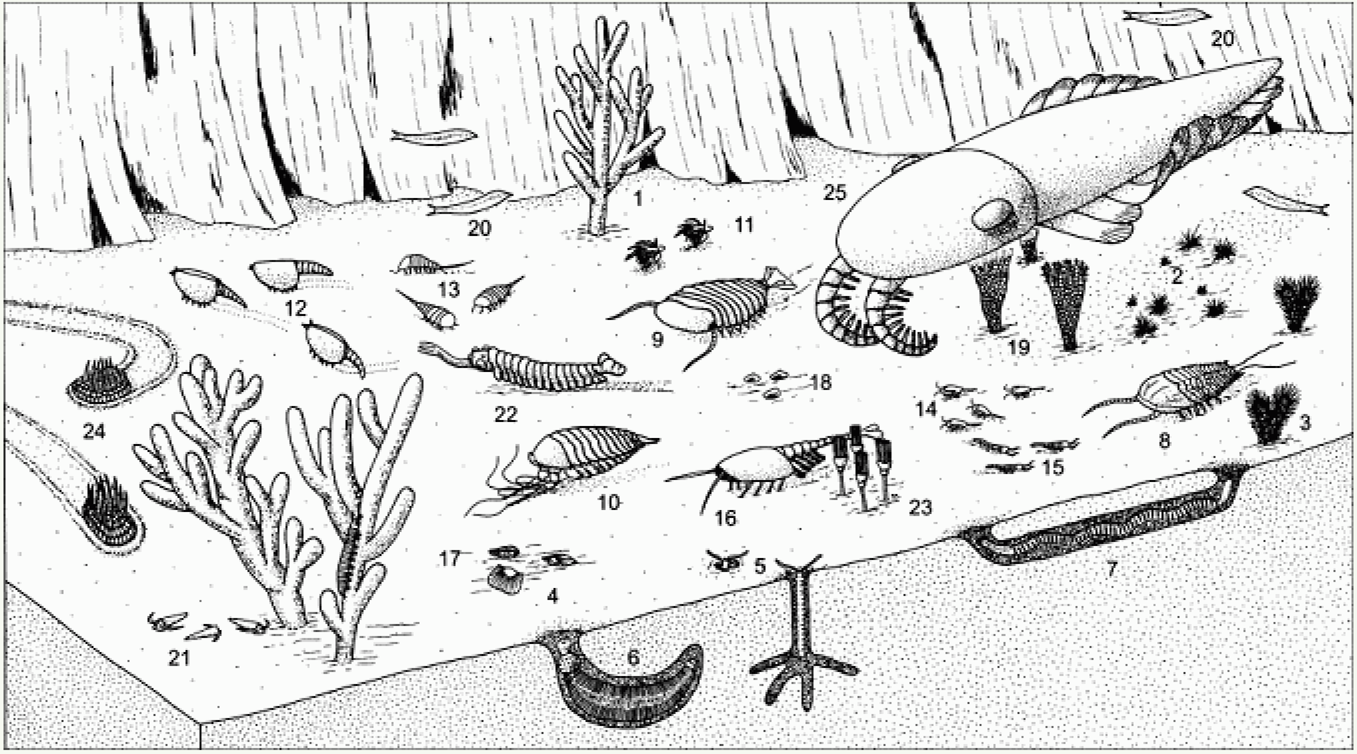
The Amgan

Cambrian Age V and the Drumian Age: ~510 to ~503 million years ago



Biota of the Burgess Shale *Lagerstätten*:
sponges *Vanuxia* (1), *Choia* (2), *Pirania* (3); brachiopods *Nisusia* (4); polychaetes *Burgessochaeta* (5); priapulid worms *Ottia* (6), *Louisella* (7); trilobites *Olenoides* (8); other arthropods *Sidneyia* (9), *Leanchoilia* (10), *Marella* (11), *Canadaspis* (12), *Molaria* (13), *Burgessia* (14), *Yohoia* (15), *Waptia* (16), *Aysheaia* (17); molluscs *Scenella* (18); echinoderms *Echmatocrinus* (19); chordates *Pikaia* (20); along with *Haplophrentis* (21), *Opabina* (22), lophophorate *Dinomischus* (23), proto-annelid *Wiwaxia* (24), and anomalocarid *Laggania cambria* (25).
from *The Fossils of the Burgess Shales*, by Briggs, Erwin and Collier, 1994)

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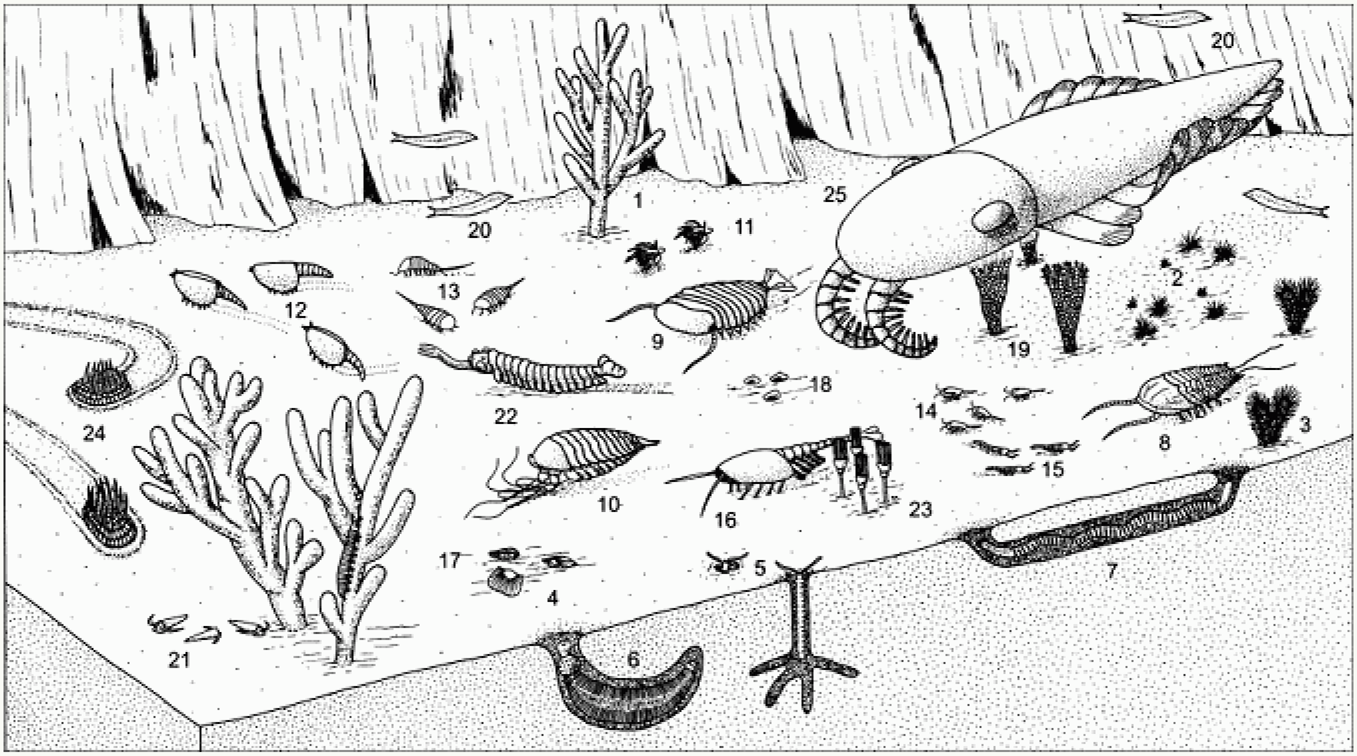
The Menevian

The Menevian Age of the Middle Cambrian Epoch: 507 to 501 million years ago



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from *The Fossils of the Burgess Shales*, by Briggs, Erwin and Collier, 1994)

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The Furongian (Late Cambrian)

The Furongian Epoch of the Cambrian Period: 501 to 488 million years ago

Paleozoic
Cambrian
Early Cambrian
Cambrian Epoch 2
Middle Cambrian
Furongian
Paiban
Cambrian Stage IX
Dolgellian
Ordovician
Early Ordovician
Middle Ordovician
Late Ordovician

Introduction
Ecosystems
Furongian Life
Links

The Late Cambrian has recently acquired an official name, the Furongian Epoch. It consists of the Paibian Age and an unnamed an Late Furongian ("Dolgellian") Age. Not coincidentally, the GSSP occurs near the Chinese village of Paibi, in the incredibly beautiful -- and almost vertical -- Wuling Mountains of northwestern Hunan Province. The Late Cambrian is marked by the first appearance of perhaps the very first agnostid trilobite, *Glyptagnostus reticulatus*, at Paibi. Agnostids are strange, rather primitive-looking trilobites. At first glance they look more like castanets than arthropods. The front and back sections of the shell (the *cephalon* and *pygidium*) are simple parabolic sheilds. The middle section (*thorax*) is segmented, but short. Like many other agnostids, *Glyptagnostus* is eyeless and quite small.

Ecosystems

During this time their evolved deeper burrowers and grazing increases, creating increasingly Phanerozoic-style substrates (poorly laminated shallow water sediments and soupy water-sediment interfaces) which led to the extinction of taxa like helioplacoids that required hard sediment-water interface. Mat scratchers and mat miners migrated upwards towards littoral (tidal and intertidal) zone and downwards to deeper water.

What�s happened here? One theory is that the

substrate was beginning to change. The Early Cambrian sea floor seems to have been compact and stiff. A number of reasons are cited for this condition. Most importantly, metazoan worms were relatively rare. In all other parts of the Phanerozoic, the upper layers of shallow seas are full of marine worms, molluscs, and tiny arthropods, constantly churning and reworking the sea floor. In the Early and Middle Cambrian, these were much less common. Algal mats penetrated the intersitices between sediment particles, fixing and stiffening the sea bottom. Given time, these mats grew into dome-shaped *stromatolites*, which are frequently found covering near-shore sea bottoms throughout the Cambrian and well into the Ordovician.

By the Furongian, metazoans had been chewing holes in this mat, and in the sea floor, for about 40 My. Some parts were beginning to resemble the loose, muddy and unconsolidated sea floor of our own day. For reasons less easily explained, the rate of weathering on land also increased, so that the amount of recently deposited sediment was, on average, also somewhat larger that in previous epochs. The larger, superficially more advanced trilobites of the Middle Cambrian would have literally dug their own graves in this new, muddier world. By contrast, the tiny, clam-like agnostids were well equipped to dig into -- and out of -- the loosened substrate.

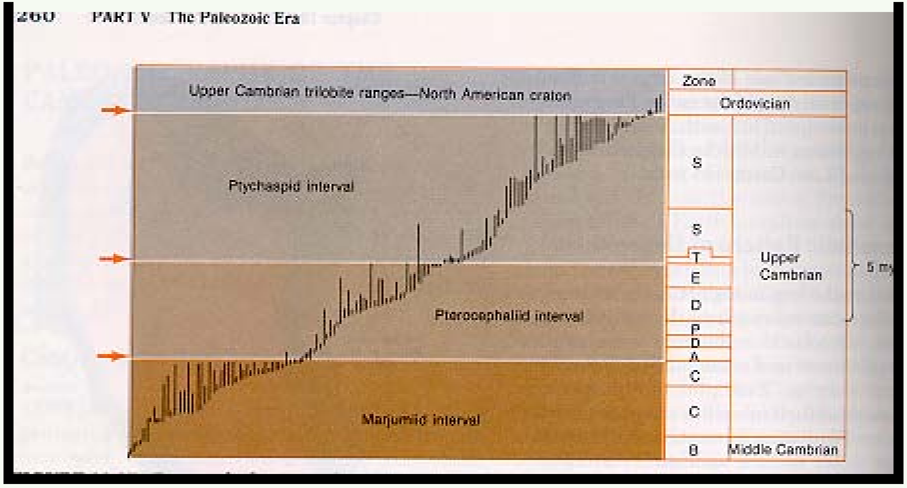
Image: *Glyptagnostus reticulatus* from **Passagen**

Furongian Life

Trilobites, brachiopods, and other typical Cambrian groups continued to flourish. molluscs diversified with the appearance of many new clades. Graptolites appear (mostly benthic forms). Also during the Late Cambrian, conodonts first appear. These were probably fast swimming micropredators, soft-bodied chordates, possibly even vertebrates, with flattened elongate eel-like bodies. They are known almost entirely from their hard (calcium phosphate) tooth-like elements (common as microfossils), but a few instances of soft tissue preservation revealed their physical form. They survived until end of the Triassic. There is currently no evidence for land plants in the Cambrian.

Extinction Events

As we might expect, the environmental changes in the Furongian led to a general turnover of organisms in the great shallow seas of the Cambrian. Many sources refer to these as "mass extinctions." However, we might reserve that term for a relatively small number of events of greater magnitude and severity. In a biotic turnover "event," most organisms are simply replaced by other organisms of a similar type. The mechanism of replacement is likely to involve a significant amount of natural selection by competition. A mass



extinction ought to mean elimination of multiple species without competitive selection, such as by a natural disaster. These are two extremes of a continuum, but it is sometimes useful to distinguish between the two mechanisms.

It appears that trilobites, and probably other groups, turned over about three times during the Furongian, with the most profound change occurring at the very end of the Cambrian. The end-Cambrian event comes much closer to to being a mass extinction. Some workers believe that the Cambrian ended with a major cooling episode – possibly even a minor ice age. We have to be somewhat careful with this sort of hypothesis. The number of biotic events which have been recently ascribed to climate changes exceeds even the number tied to extraterrestrial impacts. (We eagerly await the discovery of a mass extinction caused by a glacier from outer space.) These explanations are not necessarilly wrong, but they give off the general odor of a scientific fashion which may or may not survive more rigorous analysis.

Image: from Steven M. Stanley *Exploring Earth and Life through Time*

Other Invertebrates

Annelida: No evidence of differentiation from stem group of Coeloscleritophora (*Halkeria*, *Wiwaxia*)?

Phyllodocida may have been present since Middle Cambrian, (implying considerable cryptic development). "(see Conway Morris and Peel 1995; Fauchald and Rouse 1997)." "Outgroup comparisons imply that the plesiomorphic mode of feeding in annelids, mollusks, and the Cambrian preannelidan halkieriids is unselective microphagous grazing, in which a radula or other toothed structure loosens and gathers particles from hard surfaces and sediments" (numerous cites) Thesis is that herbivory did not constitute a major guild in the Paleozoic. Scolecodonts are not known until the Ordovician. Vermeij, GJ & DR Lindberg (2000), *Delayed herbivory and the assembly of marine benthic ecosystems*. **Paleobiology** 26: 419-430.

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The Furongian (Late Cambrian)

The Furongian Epoch of the Cambrian Period: 499 to 488 million years ago

The Late Cambrian has recently acquired an official name, the Furongian Epoch. It consists of the Paibian Age and an unnamed an Late Furongian ("Dolgellian") Age. Not coincidentally, the GSSP occurs near the Chinese village of Paibi, in the incredibly beautiful -- and almost vertical -- Wuling Mountains of northwestern Hunan Province. The Late Cambrian is marked by the first appearance of perhaps the very first agnostid trilobite, *Glyptagnostus reticulatus*, at Paibi. Agnostids are strange, rather primitive-looking trilobites. At first glance they look more like castanets than arthropods. The front and back sections of the shell (the *cephalon* and *pygidium*) are simple parabolic sheilds. The middle section (*thorax*) is segmented, but short. Like many other agnostids, *Glyptagnostus* is eyeless and quite small.

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Image: *Glyptagnostus reticulatus* from **Passagen**

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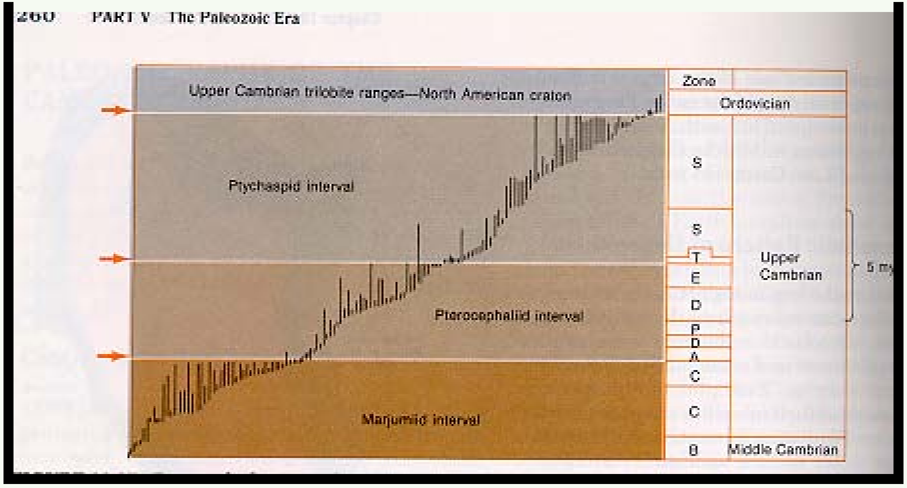

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Image: from Steven M. Stanley *Exploring Earth and Life through Time*

Other Invertebrates

Annelida: No evidence of differentiation from stem group of Coeloscleritophora (*Halkeria*, *Wiwaxia*)?

Phyllodocida may have been present since Middle Cambrian, (implying considerable cryptic development). "(see Conway Morris and Peel 1995; Fauchald and Rouse 1997)." "Outgroup comparisons imply that the plesiomorphic mode of feeding in annelids, mollusks, and the Cambrian preannelidan halkieriids is unselective microphagous grazing, in which a radula or other toothed structure loosens and gathers particles from hard surfaces and sediments" (numerous cites) Thesis is that herbivory did not constitute a major guild in the Paleozoic. Scolecodonts are not known until the Ordovician. Vermeij, GJ & DR Lindberg (2000), *Delayed herbivory and the assembly of marine benthic ecosystems*. **Paleobiology** 26: 419-430.

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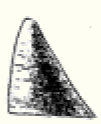
The Paiban

The Paiban Age of the Furongian Epoch: 501 to 496 million years ago

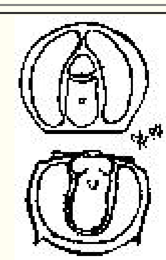
Also known as the Maentwrogian, Dresbachian and the Ffestiniogian, the Paiban is a stage of the Furongian, underlain by the Guzhangian and overlain by an unnamed Stage IX and the Dolgellian, and dated at 501 to about 496 million years ago.



Phylum : **Mollusca**
Class: **Tergomya**
Order: **Hypseloconoidea**
Family: **Hypseloconidae**

Hypseloconus elongatus *Berkey*

Size: about 2.5 to 4 cm tall
Horizon: Dresbachian
Locality: Wisconsin USA
Comments: the Hypseloconoidea, represented by species like *Hypseloconus elongatus* and *Knightoconus antarcticusse*, with cap-shaped shells (which in the case of *Knightoconus* also possessed septa), are often thought



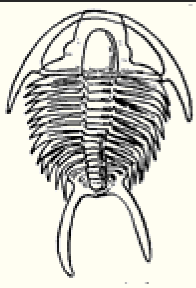
Phylum : **Arthropoda**
Class: ???**Trilobita**
Order: **Agnostida**
Suborder: **Agnostina**
Family: **Agnostidae**

Agnostus pisiformis

Size: about 5 mm long
Horizon: Early Paiban Age - *Agnostus pisiformis* zone
Locality: Sweden
Comments: Agnostid trilobites had only two thoracic segments. These tiny trilobites were planktonic drifters.

to be ancestral to the Cephalopoda, although the evidence for this is still debated
Drawing from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952, p.291

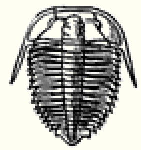
Following the discovery of a Furongian form from the Orsten Lagerst�tten with a limb preserved, it is believed now that these animals were not true trilobites at all, but more closely related to Crustacea
Drawing © *Inga B. Agnér*



Phylum : **Arthropoda**
Class: **Trilobita**
Order: **Ptychopariida**
Suborder: **Ptychopariina**
Superfamily: **Crepicephalacea**
Family: **Tricrepicephalidae**

Tricrepicephalus cedarensis *Resser*

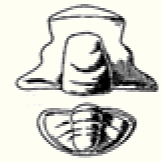
Size: about 4.5 cm wide
Horizon: Nolichucky Shale (Early Paiban Age - *Agnostus pisiformis* (European) zone / *Cedaria* and *Crepicephalus* (North American) Zones
Locality: Alabama, USA
Comments:
Drawing from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952, p.503



Phylum : **Arthropoda**
Class: **Trilobita**
Order: **Ptychopariida**
Suborder: **Ptychopariina**
Superfamily: **Olenacea**
Family: **Olenidae**
Subfamily: **Oleninae**

Olenus gibbosus *Wahlenberg*

Size: about 1.5 to 2 cm long
Horizon: *Olenus* zone (Late Paiban Age)
Locality: Sweden
Comments:
Drawing from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952, p.503



Phylum : **Arthropoda**
Class: **Trilobita**
Order: **Ptychopariida**
Suborder: **Ptychopariina**
Superfamily: **Komaspidacea**
Family: **Elviniidae**

Elvinia roemeri *(Shumard)*

Size: about 1.5 to 2 cm long
Horizon: Wilberns Formation , *Elvinia* (North American) Zone *Olenus/Agnostus obesus* zone (Late Paiban Age)
Locality: Texas
Comments: cranidium and pygdium "tail"
Drawing from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952, p.500

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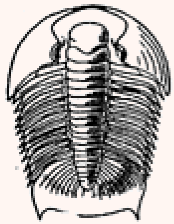
The Dolgellian Age

The Dolgellian Age of the Furongian Epoch: 492 to 488.3 million years ago



Dikelocephalus oweni Ulrich & Resser
about 7 cm long
Trempealeauan of Wisconsin (Laurentia)
Drawing from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952

The Furongian Epoch - the Dolgellian Age

The Dolgellian is not yet formally recognized by the IUGS. It represents the second half of the Furongian and lasted 2-3 million years. It is also known as the Franconian, Trempealeauan, or Marjuman-Steptoean. The Dolgellian is underlain by the Paiban and dated at 514.1-510 Myr ago by Harland et al.. However, the IUGS has fixed the end of the Cambrian at 495 mya, making the Dolgellian approximately 497 to 495 mya.

Some Dolgellian Molluscs

Phylum : **Mollusca**
Class: Gastropoda?
Order: **Bellerophontina**
Superfamily: Bellerophontoidea
Family: Sinuitidae
Subfamily: Bucanellinae

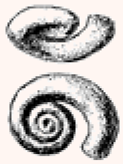
Owenella antiquata *(Whitfield)*

Size: about 1 cm diameter
Horizon: Trempealeauan,
Locality: Wisconsin
Comments: an early Bellerophont
drawing from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952, p.291

Phylum : **Mollusca**
Class: **Gastropoda**
Subclass: "Prosobranchia"
Order: **Vetigastropoda**
Superfamily: ?Pleurotomarioidea
Family: Sinuopeidae
Subfamily: Sinuopeinae

Sinuopea sweeti *(Whitfield)*

Size: about 2.5 cm tall
Horizon: Trempealeauan,
Locality: Wisconsin
Comments: an early Bellerophont
drawing from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952, p.291



Phylum : **Mollusca**
Class: **Gastropoda**
Subclass: Eogastropoda
Order: **Euomphalina**
Superfamily: Ophiletoidea
Family: **Ophiletidae** Knight, 1956

Schizopea normalis *(Ulrich & Bridge)*

Size: about 2.5 cm wide
Horizon: "Upper Cambrian" (Eminence Dolomite)
Locality: Missouri
Comments: a representative of a very primitive gastropod lineage. In this species the body whorl partially uncoiled. Although this means the shell was less protected, it is possible that the lesser number and efficiency of preditors at this time meant that the animals were not unduley disadvantaged. Later biological "arms races" would lead to more tightly coiled shells. syn: *Dirhachopea normalis*.
Drawing from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952, p.291

Eburoceras

Phylum : **Mollusca**
Class: **Cephalopoda**
Subclass "Nautiloidea"
Order: **Ellesmerocerida**
Family: **Ellesmeroceratidae**

Eburoceras sp.

Size: Length of above specimen: 7 cm
Horizon: Fengshan Formation (Late *Quadraticephalus* to *Cinoeremoceras-Acaroceras* Zones)
Locality: north-east China
Comments: one of a number of mostly small, very primitive, cephalopods from this locality
from Teichert 1988 from Chen and Teichert 1983a

A new group that appeared although still locally and in small numbers at this time were the Cephalopods (see above right). Several orders of Nautiloids - Plectronocerida, Yanhecerida, Protactinocerida, and Ellesmerocerida came upon the scene, but only the Ellesmerocerids were to survive the end Cambrian mass-extinction and give rise to the rest of the Cephalopods in the early Ordovician onwards [Teichert 1988]

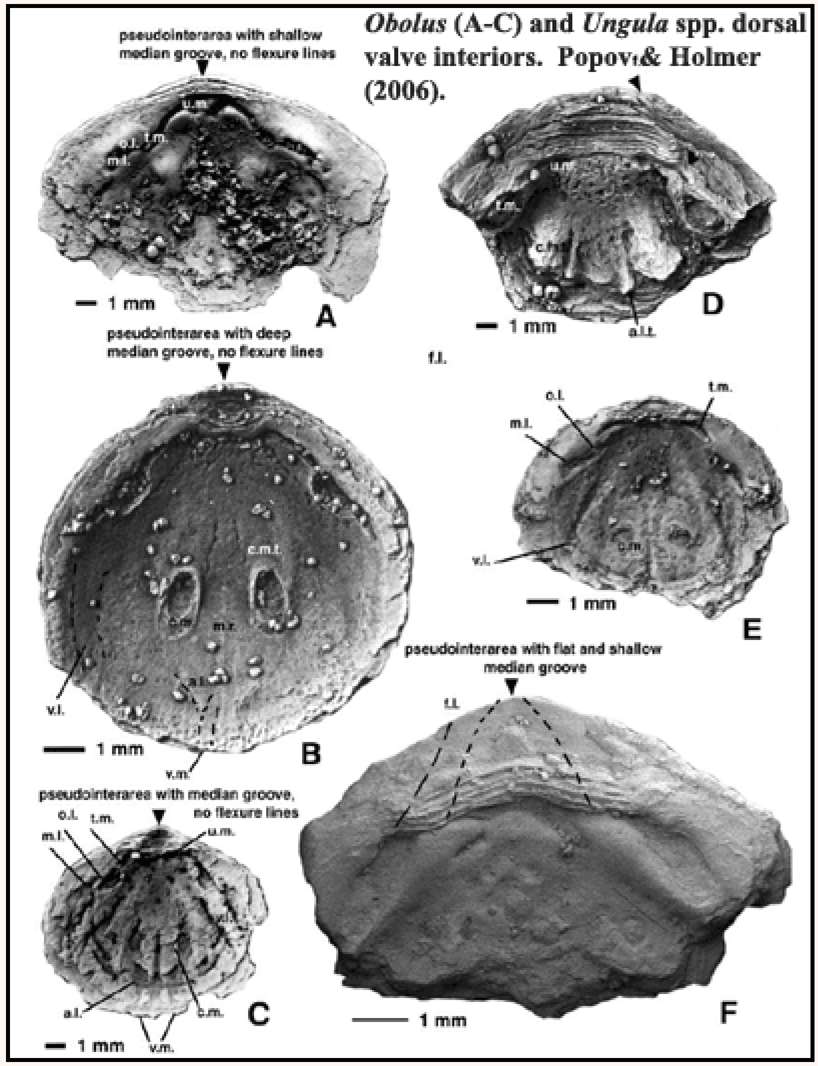
Other Invertebrates

Annelida

Work on Ediacaran forms in the 1980's suggested that *Spriggina* was a Pre-Cambrian annelid, but this now seems unlikely. Scolecodonts, parts of the complex jaw apparatus of polychaete worms, have been reported from the Furongian, but they are not common until the Late Ordovician. We understand that new Ediacaran finds may push the date back again. However, the present concensus seems to be that definitive annelids had barely differentiated from their "Procoelomate" stem by the Furongian.

Brachiopoda

Several groups of orthid brachiopods thrived during the Dolgellian, including the early protorthoids and lingulids, as well as more derived forms such as the Billingsellida and Orthodina. Lingulates were probably the most succesful brachiopod group in Dolgellian times. Relatively advanced forms, such as the siphonotretid lingulates appeared for the first time during the Furongian. They underwent a considerable expansion during the Dolgellian and included *Ungula, Obolus, Schmidtites,* and *Helmersenia*. Sturesson *et al*. (2005); Popov & Holmer (2003).



Obolus **(A-C) and** ***Ungula*** **spp. dorsal valve interiors. Popov & Holmer (2006).**

Bryozoa

No Bryozoa are known before the Early Ordovician. Possibly, in fact probably, they were present as soft-bodied forms during the Dolgellian.

Impression of Maentwrogian scyphozoan. From Haggadorn et al. (2002).

Cnidaria

Corals were just getting started during the Dolgellian, and are represented in the fossil record by a few early rugose forms. Anenomes (Anthozoa) have been described from the Early Cambrian of China, so they were undoubtedly present in the Dolgellian. However, little is known of them. Essentially modern scyphozoans (jellyfishes) have been recovered from mass-stranding events dating from the preceeding Paiban Age of Wisconsin. Hagadorn *et al*. (2002).

Echinodermata

Furongian echinoderm faunas are fairly sparse compared to those of the Middle Cambrian. They include stylophorans (only cornutes -- mitrates had not yet appeared), eocrinoids, and blastozoans (including rhombiferans) with occasional edrioasteroids and perhaps solutes. Lee *et al*. (2005). Homalozoans had undergone an extensive radiation in the Early and Middle Cambrian; but, by the Dolgellian, several of the Middle Cambrian groups had already vanished. Bottjer *et al*. (2000), in a rather influential series of papers, explain the faunal changes of the Furongian as a "substrate revolution." Because of the evolution of active infauna and mobile bottom feeders, algal and bacterial mats were replaced by bioturbated soft muds as the most common sea bottom in shallow waters. Consequently, they argue, suspension feeders were forced to adapt by attaching to hard substrates (like brachiopods), developing "root" systems for soft substrates (eocrinoids), or developing some degree of mobility (perhaps stylophorans). The Dolgellian would then represent the final stage of this transformation.

We are less happy with this theory than we once were -- not because it is wrong, but because it seems incomplete.

This is a bigger topic than we can take up here, but there are a number of global, or at least broad regional, factors (in addition to local variables) which influence substrate. These include "reef" types, sea level trends, and a number of variables influencing the type and amount of weathering (e.g. oxygen levels, temperature, volcanic activity). The Furongian is a simple case, since none of these additional factors was particularly important. However, the advent of new reef structures in the Ordovician may well have created a new type of firm, semi-organic substrate, which complicates the issue a great deal.

Porifera

Archaeocyaths, which had been on the wane since the end of the Early Cambrian, became entirely extinct shortly before or during the Dolgellian. More conventional Porifera, particularly Hexactinellida, were abundant and diverse. ATW060130.

Links

Upper Cambrian Extinction, Carbon Isotope Shifts and the Sauk II - Sauk III Sea Level Event: New Evidence from Northern Utah, Newfoundland and the Mid-continent

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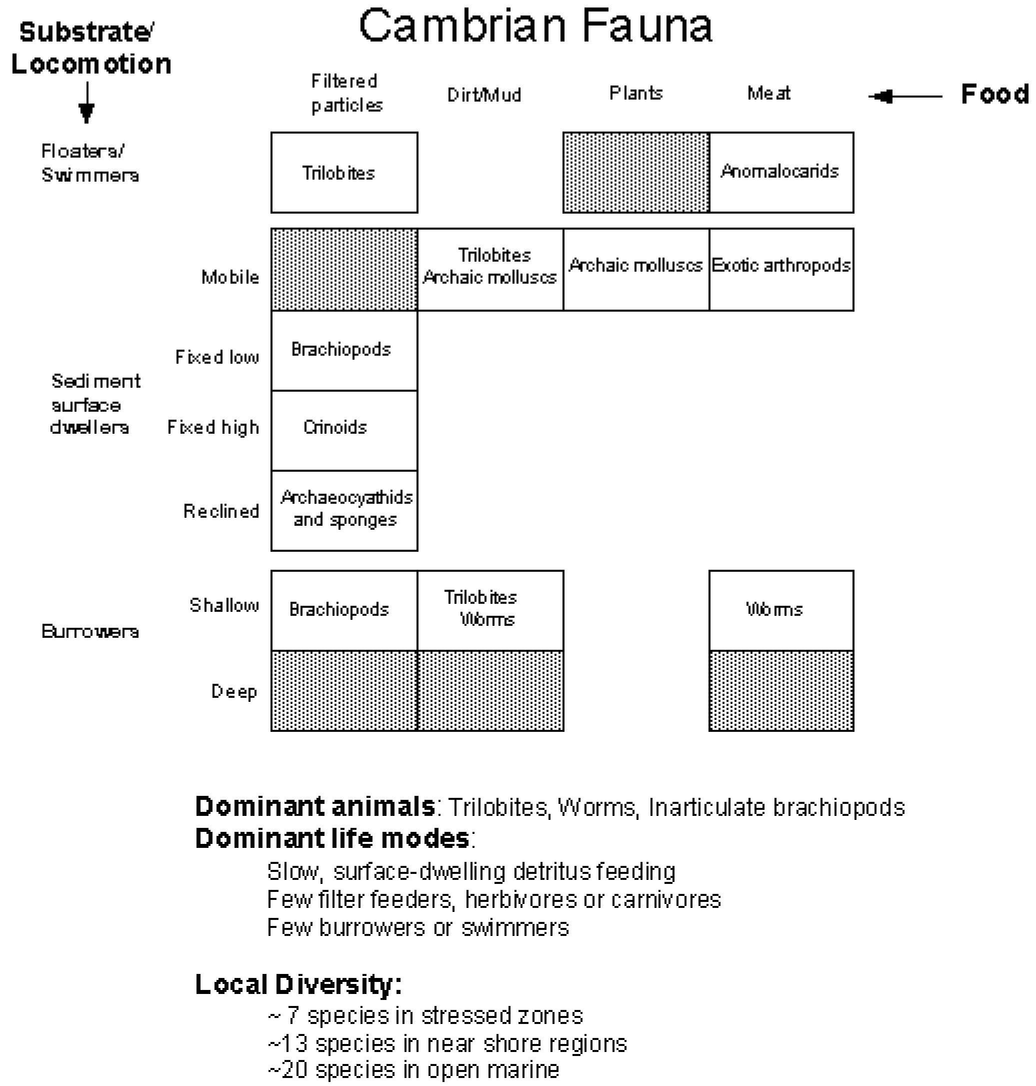
Cambrian Benthos

Following the earliest Cambrian (Tommotian) fauna, there was a rise of herbivore grazers (e.g. gastropods), and consequent decline of algal stromatolites . There were almost no large animals, and only a few predators (chiefly anomalocaridids).

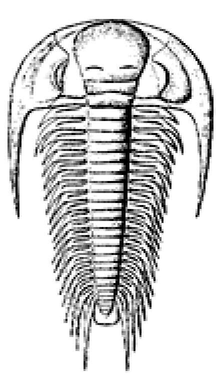
Cyanophyte algae mats encouraged mat scratchers (such as a diverse assemblage of early mollusks, previously lumped in the watebasket taxon "monoplacophora"), and some probable mat-sticking echinoderms (helioplacoids).



Cambrian faunal guilds (original url)

Most life concentrated near sediment- water interface; with only shallow burrowers and encrusters. Even so, the Cambrian benthos had already developed a simple tiering system with two levels of (0-50 mm and 50-100 mm. The lower tier was dominated by archaeocyaths, which formed small reefs (in the Early Cambrian only: there were almost no Middle or Late Cambrian reefs), echinoderms, nonarticulate brachiopods and sponges; the higher level included archaeocyaths, echinoderms (eocrinoids and crinoids) and were rare but nevertheless included some bizarre forms such, as the helicoplacoids. , Most Cambrian echinoderms were stalked (and thus sessile), but some were motile (able to crawl about)

The Cambrian saw the beginning of bioturbators, with limited vertical mining abilities. This infauna was generally shallow, burrowing close to the sediment-water interface with the exception of vertical *Skolithos* burrows, which were often deep.



left - *Paradoxides* - a large trilobite
(length upto 45 cm)

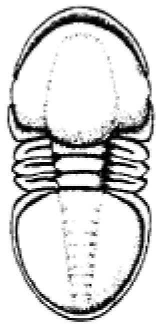
Trilobites dominated the mobile benthos, accounting for over 50% of Cambrian hard-shelled species. They were mostly benthic epifaunal detritovores (possessing a backwards facing mouth); detritus-feeders crawling across or swimming above the sea-floor, whereas some may have lived in shallow burrows. Both body and trace fossil representatives of the trilobites are common in Cambrian strata. They are known from many growth stages, thousands of species, and trace fossils. The functional morphology of the Furongian olenids indicates the already sophisticated design of the Cambrian Trilobita.

Brachiopods included "inarticulates"; both linguates (infaunal forms with calcium phosphate shells) and craniids epifaunal forms with calcite shells). Articulate brachiopods (epifaunal with calcite shells) are present but rare

ref: Benchley and Harper, *Palaeoecology*, p.125

Nekton and plankton

Paleozoic **Cambrian** **Early Cambrian** **Middle Cambrian** **Late Cambrian**	**Home** **Cambrian Period** **Cambrian Lagerstätten** Cambrian Nektonic Marine Ecosystems Cambrian Terrestrial Ecosystems **References**



Pagetiellus
a planktonic (nektonic) agnostid trilobite
early Cambrian period

note: the following passage is from Benchley and Harper, *Palaeoecology*, pp.125-8

Relatively little is known of Cambrian nekton. Some molluscs such as the hyoliths may have been pelagic, together with primitive jawless fishes. The Cambrian plankton was more abundant and diverse than that of the Precambrian oceans. The acritarchs radiated during the Cambrian, radiolarians occupied tropical latitudes, whereas chitinozoans were present in Cambrian plankton but not abundant. Larval phases of benthic organisms together with the agnostic trilobites (illustration above) dominated a zooplankton still apparently free of macrophagous predators.

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Cambrian Lagerst�tten

Most Cambrian organisms are only known from their hard parts, but a number of exception sites preserve soft-tissue impressions. Here is a partial listing of Cambrian Lagerst�tte

Some Cambrian Lagerstätten	Location	Period/Epoch	Age of Deposits	Type of organisms
Sirius Passet	,	Early Cambrian (Atdabanian)	521 million years old	mostly soft-bodied arthropods, also annelids and large priapulids; few taxa with shelly skeletons
Chengjiang	Yunnan Province, China	Early Cambrian (Latest Atdabanian or earliest Botomian?)	519 million years old	many different groups well represented
Burgess Shale	British Columbia, Canada	Middle Cambrian (Amgan)	507 million years old	many different groups well represented
Orsten	Sweden	Late Cambrian	495 million years old	various tiny (mostly larval) arthropods

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Chengjiang

Lower Cambrian soft-tissue fossils from Chengjiang, near the city of Kunming in Yunnan Province, China, preserve a diverse biota dated approximately 515 to 520 Ma, some 25 Ma after the beginning of the Cambrian and pre-dating the Middle Cambrian Burgess Shale by perhaps 10 to 15 Ma (Martin *et al*. 2000), and thus encoding an early record of the Cambrian Explosion.

The - - ied fossils include "diverse algae, medusiform metazoans, chondrophorines, sponges, chancelloriids, sea anemones, priapulid worms, hyoliths, possible ectoprocts, inarticulate brachiopods, annelid-like animals, lobopodians, trilobites and non-trilobitic arthropods, hemichordates and probable earliest chordates as well as taxa that cannot definitely be assigned to any well established groups" (International Subcommission on Cambrian Stratigraphy).

The fossils occur in rocks of the Qiongzhusi Formation, cropping out at Maotianshan near Chengjiang, Yunnan Province, South China (fig. 1) where they were accidentally discovered in 1984.

Geological Setting

The fauna derives from the long-known Qiongzhusi Formation (syn. "Chiungchussu") of the Qiongzhusi Stage of the late Early Cambrian.

The sediments are finely laminated mudstones, formed in an outer shelf detrital belt, in quiet water environments. The frequency of macrobenthos suggests that the water was relatively well oxygenated, although bioturbation is sparse so that possibly only the uppermost layer at the sediment surface was oxygenated.

The preservation of non-mineralized organismal parts probably resulted from repeated rapid burial events that prevented the bodies from destruction by currents, bioturbation and other biotic activities such as by scavengers and carnivores. Burial is also thought responsible for absence of sulphate reduction which apparently was low so that the soft-parts were preserved in a number of different layers in the formation. Well developed anoxic conditions are reflected by several layers with carbon-rich deposits in the Qiongzhusi Formation. These conditions probably led to frequent mass mortalities which may have played a significant role in the soft-part preservation.

Fig. 1: Map showing approximate location of the Chengjiang fossil beds in Yunnan, southern China.

Biota

The Chengjiang biota occurs about 25 m above the earliest trilobites (genus *Parabadiella*) found in this area and on the Yangtze Platform (which are most probably coeval to late Atdabanian trilobites of the Siberian Platform).

Perhaps the most surprising aspect of the Chengjiang biota is the wealth of taxa from so many different groups. The fossil assemblages includes diverse algae, medusiform metazoans, chondrophorines, sponges, chancelloriids, sea anemones, priapulid worms, hyoliths, possible ectoprocts, inarticulate brachiopods, annelid-like animals, lobopodians, trilobites and non-trilobitic arthropods, hemichordates and probable earliest chordates as well as taxa that cannot definitely be assigned to any well established groups.

It is not only the diversity and early appearance in the fossil record which makes the Chengjiang assemblage fabulous, but also the fine preservation which offers the opportunity to learn more about the morphology of these early creatures. One of the most outstanding examples might be *Microdictyon*, the isolated sclerites of which were known from numerous localities on various continents, but none of the specialists had any idea how this creature could have been organized. The discovery of these net-like scales of Microdictyon on a worm-like animal resolved the question.

Phylum Porifera

Class Demospongiae

Sponges are a major component in Lower Cambrian Chengjiang fauna, where they are second only to arthropods in both generic and specific diversity. About 1000 sponge body fossils, distributed among 15 genera and 30 species, have been collected there. The skeletons in most species are represented exclusively by *diactines*, which form a regular, reticulate skeletal framework. The dermal reticulate organization of spicules is common in the Chengjiang fauna, and these fossils are classified as demosponges. The data from Chengjiang fauna demonstrate that main clade of early sponges, the *monaxonid* Demospongiae was diverse in the Lower Cambrian. We thus suggest that diactines evolved before other types of spicules. The keratosal demosponges that have skeletons composed entirely of spongin fibers, are seen first in the Lower Cambrian in Chengjiang fauna (Li *et al.* 1998)

Phylum Arthropoda Siebold & Stannius 1895

Subphylum Schizoramia

Superclass Arachnomorpha

Class Trilobita Walch 1771

Order Redlichiida Richter 1932

Eoredlichia intermedia

Fig. 2: *Eoredlichia intermedia* with preserved antennae and mid-gut diverticula (dark blobs in the anterior part of the rhachis). Qiongzhusi Formation, Chengjiang. [Image courtesy of Dr. Gerd Geyer, Institut f�r Pal�ontologie, Bayerische Julius-Maximilians-Universit�t, W�rzburg, Germany.]

Superclass Crustacea

Chuandianella ovata

"In 1912, Charles D. Walcott erected the Family Waptiidae to accommodate *Waptia fieldensis*, a still poorly understood bivalved arthropod from the Middle Cambrian Burgess Shale of British Columbia, Canada. Several other bivalved arthropods seemingly similar to *Waptia* have since been discovered, such as the Lower Cambrian taxa *Pauloterminus spinodorsalis* (nomen nudum) from the Sirius Passet fauna of North Greenland and *Chuandianella ovata* from the Chengjiang fauna of southwest China.

"Despite their overall waptiid-like appearance, however, each of these animals possesses features which suggest their apparent similarity to *Waptia fieldensis* may be superficial. Variability in segment number, limb number and limb type between these taxa, for example, suggests these animals may not in fact be closely related.

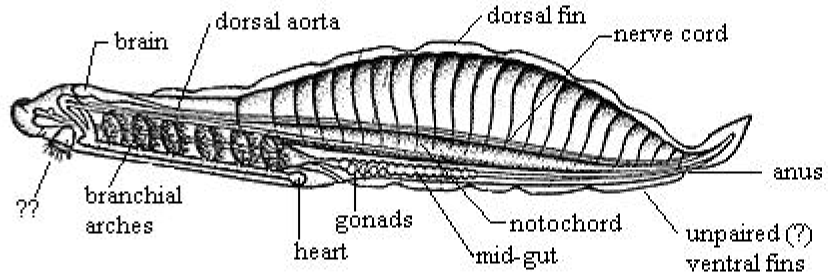
"Other non-waptiid Cambrian arthropods also possess bivalved carapaces, including the Burgess Shale taxa *Canadaspis perfecta* and *Plenocaris plena*. This indicates two alternative evolutionary scenarios. First, the relatively common occurrence of bivalved carapaces may indicate a stem-group clade of bivalved arthropods in the Cambrian, united (at least) by their possession of this specialized carapace. A second, perhaps more likely, possibility is the occurrence of evolutionary convergence, resulting in the presence of a bivalved carapace in multiple unrelated Cambrian arthropod taxa."

Phylum Chordata

Subphylum Vertebrata

Shu *et al.* (1999)

Chen *et al.* (1999)



***Haikouella lanceolata*: modified from Chen et al. (1999)**

The first fossil chordates are found in deposits from the Cambrian period (545-490 million years ago), but their earliest record is exceptionally sporadic and is often controversial. Accordingly, it has been difficult to construct a coherent phylogenetic synthesis for the basal chordates. Until now, the available - ied remains have consisted almost entirely of cephalochordate-like animals from Burgess Shale-type faunas. Definite examples of jawless fish do not occur until the Lower Ordovician (475 Myr BP), with a more questionable record extending into the Cambrian. The discovery of two distinct types of craniate-like chordates from the Lower Cambrian Chengjiang fossil-Lagerst�tte is, therefore, a very significant extension of their range. One form is lamprey-like, whereas the other is closer to the more primitive hagfish. These finds imply that the first fishes may have evolved in the earliest Cambrian, with the chordates arising from more primitive deuterostomes in Ediacaran times (latest Neoproterozoic, 555 Ma), if not earlier.

Links

Links

International Subcommission on Cambrian Stratigraphy

Chengjiang Maotianshan Shales Fossils

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Sirius Passet Lagerst�tten

The Sirius Passet fauna (named after the Sirius sledge patrol that operates in North Greenland) derives from the Buen Formation, exposed on the eastern shore of J.P. Koch Fjord in the far north of Greenland (fig. 1).

It was discovered in 1984 by A. Higgins of the Geological Survey of Greenland. A preliminary account was published by Conway Morris *et al.* (1987), but since then, three expeditions led by J. S. Peel and Simon Conway Morris have returned to the site, in 1989, 1991 and 1994, and a field collection of perhaps 10,000 fossil specimens has been amassed.

The fauna is inevitably compared to that of the Burgess Shale, although it is probably ten to fifteen million years older – 518 vs. 505 Ma (Martin et. al. 2000) – and more closely contemporaneous with that from Chengjiang.

Geological Setting

The Sirius Passet soft-body fossils are found in rocks of the Lower Cambrian Buen Formation, in mud shales, representing a rather deeper water facies than the Burgess Shale, formed on the outer continental shelf, off-shore from a carbonate escarpment. "Large chunks from the edge of the carbonate platform occasionally fell or slid into the adjacent basin, where the Sirius Passet fauna lived" (Conway Morris 1998, p. 117).

Fig. 1: Locality map showing approximate location of the Sirius Passet location on the eastern side of J.P. Koch Fjord.

Biota

Discussion of early metazoan evolution has for many years been dominated by fossil evidence from the Middle Cambrian Burgess Shale and, in particular, by its famous problematic arthropods – *Anomalocaris*, *Leancoila*, *Opabinia*, and so on." (Budd 1997, p.125). The Sirius Passet fossils are approximately ten to fifteen Ma older than those of the Burgess Shale, presenting us with an even earlier window upon metazoan evolution; a glimpse of forms which, if anything, are even more challenging to interpret.

As in the Burgess Shale and Chengjiang assemblages, arthropods are the most abundant component of the Sirius Passet fauna although there is only one or two species of trilobite whereas there are more at Chengjiang and twelve or so in the Burgess Shale. In fact there are generally few taxa having shelly skeletons; the trilobites, "rare hyoliths, a number of sponges with prominent spicules, a few small brachiopods, and no echinoderms or molluscs" (Conway Morris 1998, pp. 120-121). Of the arthropods lacking calcified exoskeletons, some are somewhat – but not markedly – similar to Burgess Shale species. Many are large, reaching 50 cm or more in length. In addition there are a number of polychaete annelids and large priapulids (*ibid.*)

In general, preservation of the Sirius Passet fossils is not spectacular.

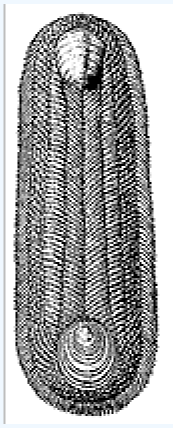
A few of the Sirius Passet taxa are described below.

Phylum Uncertain

Class Coeloscleritophora Bengtson & Missarzhevsky, 1981

Order Sachitida

Family **Halkieriidae**



Halkieria evangelista

Phylum Arthropoda

Subphylum "Protoarthropoda"

Class Dinocarida Collins 1996

Order Radiodonta Collins 1996

Family Unspecified

Kerygmachela

Kerygmachela kierkegaardi Budd 1998

Family Unspecified

Pambdelurion whittingtoni Budd 1997

Another Anomalocaridid-like taxon, but with annulated and flexible spinose frontal appendages. No eyes are known. The 'Peytoia' mouthpart is poorly sclerotised. The trunk bears lobopodous paired limbs, probably unconnected to the lateral flaps. The tail is poorly known but apparently consisting of a sub-circular flap.

Subphylum Schizoramia

Superclass Arachnomorpha

Class Trilobita Walch 1771

Order Redlichiida Richter 1932

Suborder Olenellina Walcott 1890

Family Nevadiidae Hup� 1953

Genus *Buenellus* Blaker 1988

Glabella slightly tapered forward; ocular lobe small, posterior tip about opposite S1 or anterior part of L1; width (tr.) of interocular area equal to or greater than that of extraocular area. Thorax with 17 or 18 segments, maintaining width or widening slightly backward to 8th segment, then tapering posteriorly; posterior segment may be fused with anterior part of simple pygidium; pleural spines short (exsag.); inner pleural regions only slightly wider (tr.) than axis.

The species found in the Sirius Passet assemblage is *Buenellus higginsi* Blaker 1988.

Kleptothule rasmusseni Budd 1995

Author(s): Budd, G. E.
Year: 1995
Title: Kleptothule rasmusseni gen. et sp. nov.: an ?olenellid-like trilobite from the Sirius Passet fauna (Buen Formation, Lower Cambrian, North Greenland)

Superclass Crustacea

Pauloterminus spinodorsalis (nomen nudum)

"In 1912, Charles D. Walcott erected the Family Waptiidae to accommodate *Waptia fieldensis*, a still poorly understood bivalved arthropod from the Middle Cambrian Burgess Shale of British Columbia, Canada. Several other bivalved arthropods seemingly similar to *Waptia* have since been discovered, such as the Lower Cambrian taxa *Pauloterminus spinodorsalis* (nomen nudum) from the Sirius Passet fauna of North Greenland and

Chuandianella ovata from the Chengjiang fauna of southwest China.

"Despite their overall waptiid-like appearance, however, each of these animals possesses features which suggest their apparent similarity to *Waptia fieldensis* may be superficial. Variability in segment number, limb number and limb type between these taxa, for example, suggests these animals may not in fact be closely related.

"Other non-waptiid Cambrian arthropods also possess bivalved carapaces, including the Burgess Shale taxa *Canadaspis perfecta* and *Plenocaris plena*. This indicates two alternative evolutionary scenarios. First, the relatively common occurrence of bivalved carapaces may indicate a stem-group clade of bivalved arthropods in the Cambrian, united (at least) by their possession of this specialized carapace. A second, perhaps more likely, possibility is the occurrence of evolutionary convergence, resulting in the presence of a bivalved carapace in multiple unrelated Cambrian arthropod taxa." (Taylor 1999)

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Orsten Lagerst�tten

Paleozoic
Cambrian
Terreneuvian
Fortunian
Tommotian
Cambrian Epoch 2
Atdabanian
Botomian
Middle Cambrian
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Guzhangian
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References

Links

'Orsten' Research and Dieter Waloszek's View of Arthropod and Crustacean Phylogeny - includes info on arthropods from this important but less well-known late Cambrian Lagerst�tten - **best on the Web**

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Ordovician period

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Ordovician Period

The Ordovician

The Ordovician Period of the Paleozoic Era: 488 to 444 million years ago

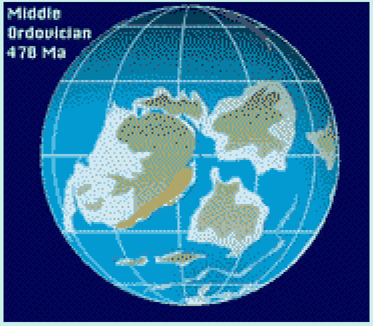
The Ordovician Period is the second period of the Paleozoic Era. This important period saw the origin and rapid evolution of many new types of invertebrate animals which replaced their Cambrian predecessors. Primitive plants move onto land, until then totally barren. The supercontinent of Gondwana drifted over the south pole, initiating a great Ice Age that gripped the earth at this time. The end of the period is marked by an extinction event.

The Ordovician System of strata was founded by Lapworth in 1879 to resolve the Murchison-Sedgwick conflict over their overlapping claims for their Silurian and Cambrian systems. Benton & Harper (1997). The name "Ordovician" comes from an ancient Celtic tribe that once inhabited the region in Wales where rock strata of this period occur.

The Ordovician was originally divided into two epochs, Bala and Dyfed. More recently, the Tremadoc was removed from the Cambrian and a three-fold division of Ordovician strata instituted.

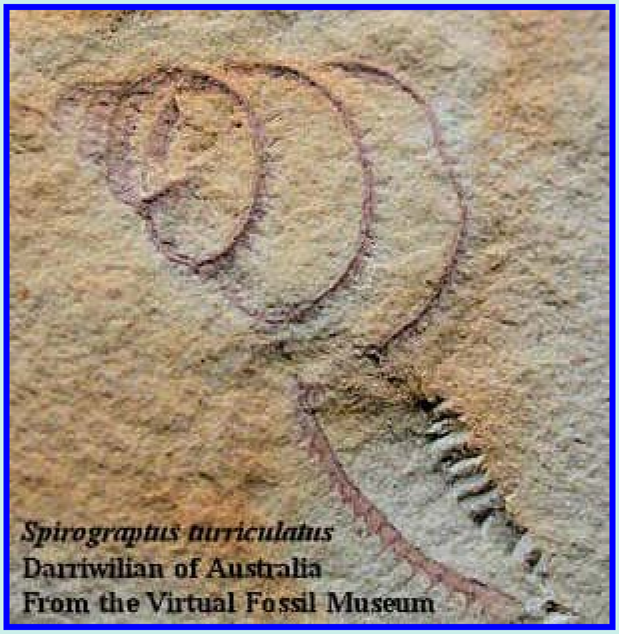
Image: An Ordovician drama - an endocerid cephalopod captures a trilobite. From **Earth History Resources**.

Ordovician Geography



During the Ordovician, Southern Europe, Africa, South America, Antarctica and Australia remained joined together into the supercontinent of Gondwanaland, which had moved down to the South Pole. North America straddled the equator, and was about 45 degrees clockwise from its present orientation. Western and Central Europe were separate from the rest of Eurasia, and were rotated about 90 degrees counterclockwise from their present orientation, and was in the southern tropics. North America is engaged in a slow collision with the microcontinent of Baltica, which forms the core of what is later to become Europe. The Iapetus Ocean continues to shrink as the previously passive margins of Baltica and North America converge. Where the Iapetus was, mountains are thrust up, remnant strata of which remain today in Greenland, Norway, Scotland, Ireland and north-eastern North America. Scotland and England are united into a single landmass.

Ordovician Stratigraphy


Spirograptus turriculatus
Darriwilian of Australia
From the Virtual Fossil Museum

The Ordovician is, from the point of view of stratigraphers, the Age of Graptolites. Graptolites are thought to be the remains of hemichordates of some kind, and often look like a cross between a conodont and a crumpled pipe-cleaner. Like conodonts, their remains are common and correlate reasonably well over broad areas of the world. The base of the Ordovician is the level at which planktonic (thus widespread) graptolites are first found. The end of the Ordovician (i.e., the base of the Silurian) corresponds to an extinction which eliminated all but one graptolite genus **[3]**.

In the last century, the gold standard in Ordovician stratigraphy was the British system. If nothing else, the Ordovician System of Britain, with its wonderful Welsh names, dated back to the dawn of geology. However, after intense study by the International Commission on Stratigraphy, it became depressingly clear that the whole thing would have to be redone if there was to be any hope of worldwide correlation for the Ordovician.

As a result, all of the age names have now been changed (except the Tremadoc) and given more rigorous definitions. However, outside the world of stratigraphers, the scientific literature still primarily uses the old names. Hence, we provide some general equivalences. Note that a few of the approximate British "equivalents" are very approximate indeed. In particular, the Arenig included not only the Floian and the Dapingian, but also the first ~2 My of the Darriwilian. Mitchell *et al*. (1997).

Note that the current (080216) versions of the Wikipedia entries on the Ordovician show a different, internationalized, version of the British system, in which the base of the Llanvirn is dragged down to coincide with the base of the Middle Ordovician. In this version, the Llanvirn occupies almost all of the Middle Ordovician except for a brief Llandeilo Age at the end. There is no room in this system for the Arenig, as it was usually understood, and the Wikipedia entries consequently avoid the use of that term.

Our representation of the British system is also bastardized, but in a different way. The term Llandeilo is indeed still frequently found, and the Llandeilo was one of the original Ordovician series, lying between the Llanvirn and Caradoc (i.e. at the top of the Middle Ordovician). In many versions of British Ordovician stratigraphy, the Llandeilo was merged with Llanvirn even before the ICS started playing with the whole system. This is the representation we have adopted, because it allows us to show the Arenig as it was used during most of the XXth century. Accordingly *we* avoid using the term *Llandeilo*. This discussion may give you a good understanding of why the ICS thought it better to start all over again when it began to address Ordovician stratigraphy.

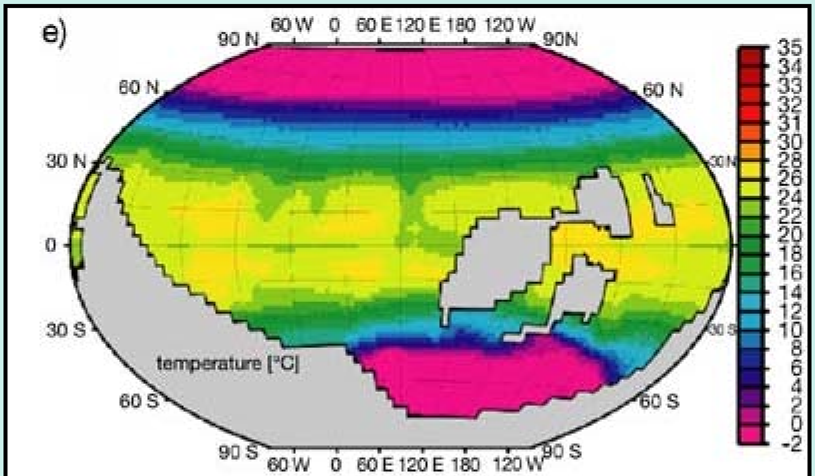
Period	Epoch	Age	Approx. British	Base	Duration

			Equivalent		
Silurian	**Llandovery**	**Rhuddanian**		**443.7**	**4.7**
Ordovician	**Late Ordovician**	**Hirnantian**	**Ashgill**	**445.6**	**1.9**
		Katian	**Caradoc**	**455.8**	**10.2**
		Sandbian		**460.9**	**5.1**
	Middle Ordovician	**Darriwilian**	**Llanvirn (& Llandeilo)**	**468.1**	**7.2**
		Dapingian	**Arenig**	**471.8**	**3.7**
	Early Ordovician	**Floian**		**478.6**	**6.8**
		Tremadoc	**Tremadoc**	**488.3**	**9.7**
Cambrian	**Furongian**	**Cambrian X**		**492.0**	**3.7**

Ordovician Climate

glaciation

A major transgression in the Middle Ordovician created widespread shallow, warm epicontinental seas. Thus, most of the Ordovician was favorable for marine life, particularly around the well-studied European and North American cratons. However, the Ordovician ended in a brief (300-500 ky), but severe, ice age. Gondwana, particularly Africa, straddled the South Pole and became extensively glaciated. There were even glaciers in what is now the Sahara. Metazoans were severely effected. About 60% of animal genera became extinct, making this the second or third most deadly mass extinction of the Phanerozoic **[1]**.



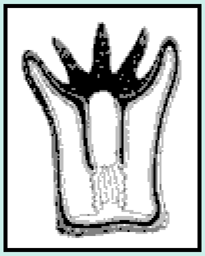
Sea-surface temperatures predicted for Late Ordovician with 8x CO_2 and low sea levels. Hermann *et al.* (2004).

As a natural consequence, a good deal of attention has been focused on the causes of the Ordovician Ice Age. In fact, it is not easy to see how an ice age could have occurred. Atmospheric carbon dioxide levels are believed to have been 8 to 20 times their current values. This ought to have prevented anything approaching an ice age. Sea levels were high through most of the Ordovician. They dropped, dramatically (about 50 m), in connection with the ice age, but it is hard to tell whether this was cause, effect, or both. One independent factor which would affect both pCO_2 and sea level is the rate of sea floor spreading along mid-ocean ridges. As we might expect, the length of well-established mid-ocean ridges, i.e., the ridge between Gondwana, to the south, and Baltica plus Laurentia, to the north, was unusually short during the Late Ordovician. A former ridge between the two northern continents became inactive about this time. However, there may have been a very long ridge to the Northwest of Laurentia. The information is too sparse to be certain. In any event, the absence of active ocean crust formation would only affect the rate of CO_2 outgassing, not the rate at which it was locked away in sediments.

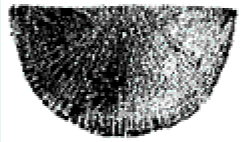
The state of the art in mathematical modeling of the problem is described in the recent work of Hermann *et al*. (2004). The results are frustratingly uninformative. Sea surface temperatures for the later Ordovician are extremely sensitive to atmospheric carbon dioxide levels and to not much else. Even the changes in geography, which brought more land surface close to the South Pole, seem to have little effect on the outcome. The result in the image indeed predicts glaciers in Gondwana at the end of the Late Ordovician. Unfortunately, it also predicts glaciers in Gondwana at the *beginning* of the Late Ordovician, even with much higher sea levels. Thus, if the models have anything to tell us, it is that there must have been a very strong draw-down of CO_2 over the Late Ordovician. No one, at this point, has been able to offer evidence suggesting a plausible agent which would remove roughly half of all atmospheric carbon dioxide in 10-15 My.

Ordovician Life

The Ordovician was an age of evolutionary experimentation, in which new organisms evolve to replace those that died out at the end of the Cambrian. It was also one of the largest adaptive radiations in the Earth's history. The number of families of known marine invertebrates (mostly hard shelled forms, as - soft-bodied types rarely left fossils) increases from about 200 at the end of the Cambrian to around 500 in the early Ordovician. The widespread shallow, warm continental seas were the perfect environment for many groups of organisms. Micro-organisms such as colonial blue-green algae - stromatolites - are widespread. Foraminifera (marine amoebas which build tiny shells) evolve for the first time. Organisms called acritarchs, although existing during the Precambrian, become more common. Stromatoporoids (possibly sponge-like organisms) also appear.



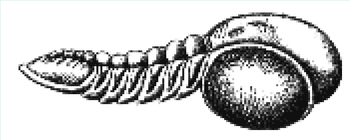
An interesting phenomenon is the sudden increase in filter feeding organisms. Cambrian animals were predominately crawling mud-grubbers and detritivores with a few swimming and burrowing predators thrown in. Filter feeders (such as *Dinomischus* and *Lepidocystis*) although an important part of the fauna, had not been exceedingly common. In the Ordovician an increase in the amount of micro-plankton would be the obvious explanation for the sudden increase in number and diversity of filter-feeders. Groups absent or under-represented in the Cambrian suddenly become more important. We see the first appearance of the corals, including both rugose and tabulate forms, bivalve molluscs, and the planktonic graptolites (creatures distantly related to vertebrates). [note: the orange anemone-like animals in top-right of the underwater scene at the top of this page are rugose corals, possibly *Streptelasma* or *Lambeophyllum*.].



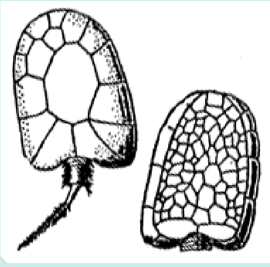
The lophophorates (animals that suck food from the water using a special fringe of tentacles around the mouth) are more filter feeders that do well in the Ordovician. The Bryozoa appear in large numbers, and constitute the most predominant colonial animals of the time. Each bryozoan polyp is a tiny creature, not unlike a coral animal. Their distant cousins the hard-shelled brachiopods are also successful. After humble Cambrian beginnings the articulate brachiopods greatly increase in diversity and abundance, with no fewer than fourteen new superfamilies. The Orthid and Strophomenid orders were especially diverse.

Among the molluscs were newcomers such as bivalves, which were not common during this time, although the Furongian Archaeogastropods develop at a moderate pace. A much more spectacular success story were the nautiloid cephalopods. Small and rare in the Furongian, the nautiloids evolve quickly along many different lines. At least ten different orders flourished at this time, all but one appearing for the first time during the early or middle part of the Ordovician. This astonishing diversity included straight-, curved, loosely coiled, and tightly coiled shelled types, and even one group (the Ascocerids) that in order to become lighter and more streamlined lost the a large part of their shell altogether. These intelligent carnivorous molluscs replaced the Cambrian Anomalocarids as the dominant life form and top predator of the world's ocean. The biggest, such as the endocerids (see graphic at top of page), attained huge size; with shells of upto 10 meters in length they were the largest animal that, up until that time, had ever lived.

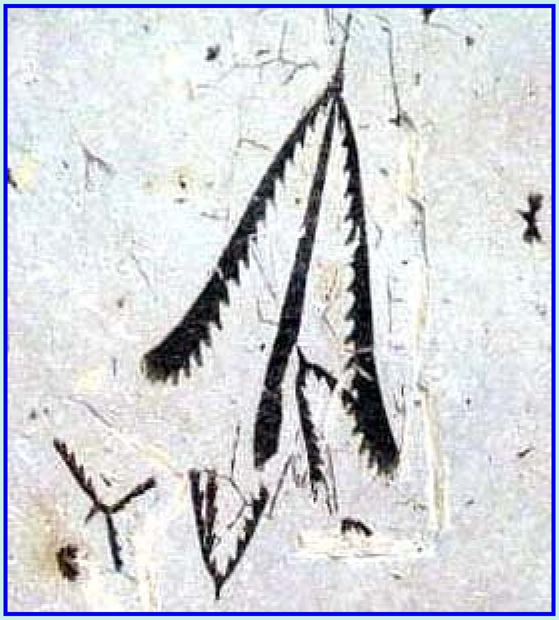
Ordovician trilobites were for the most part quite different from their Cambrian predecessors. Many evolved bizarre spines and nodules, others, such as *Aeglina prisca* (left) from the warm shallow seas of what is now Bohemia, were clearly pelagic nektonic



swimming forms, and developed huge eyes with over a thousand facets, while still others went the other direction and lost their eyes altogether. Some trilobites developed shovel-like snouts for ploughing through mud, others fused the segments of their bodies, while the curious Trinucleids developed a broad pitted margin around the head shield.



A number of early echinoderm experiments die out, others straggle on, while still others increase in diversity. The echinoderms included both a great many stalked (filter-feeding) and a few mobile (some predatory) forms. Among the bizarre forms were the carpoids, which were able to push themselves along the mud by means of a stout "tail". It has even been suggested that certain carpoids are ancestral to the vertebrates, but in view of the Furongian vertebrate origin this is unlikely. During the Ordovician the Crinoids, rare during the Cambrian, suddenly appear and diversify in large numbers. Like the brachiopods these sessile benthic (attached bottom-living) invertebrates were to become an important group of filter feeders throughout the rest of the Paleozoic.



The Ordovician was the high point of the graptolites. These colonial hemichordates possessed an anatomical structure suggestive of a portion of a spinal cord. They were vertebrate cousins rather than vertebrate ancestors. They evolved from benthic attached Furongian forms and diversified in a number of different planktonic types, including single-branched single and double rowed colonies, two-branched, four-branched, and even spiral forms.

The vertebrate ostracoderms remain rare, although several different groups of Pteraspidomorphi evolve. Their cousins the conodont animals, worm-like or eel-like organisms known mostly from numerous isolated denticles (which were used to support some kind of grasping or breathing structure in the mouth or throat) represent a major component, quite possibly predators and certainly nektonic/pelagic, in the marine food-chain.

Finally, a humble start to a new adventure: during the Ordovician the first creeping lichens and hepatophytes move onto land, the beginning of a great new experiment of life.

Image: The graptilite *Tetragraptus* from Prehistoric Life (the Victoria Museum).

Biogeography

The isolated and drifting continents serve as island arks, on the continental shelves of which marine organisms engage in evolutionary experiments. There are two main geographical provinces, a northern, equatorial tropical one, and a southern cool-water one centered around Gondwanaland. In the case of trilobites, North America and northwestern margins of Europe, Spitzbergen, Siberia and north-east Russia are characterized by a diverse fauna that H. B. Whittington calls the Bathyurid fauna. This includes trilobites of the families Bathyuridae, Hystricuridae, Asaphidae, Komaspididae, Remopleurididae and Pliomeridae. A subprovince around Baltica bathyurids and pliomerids are rare and asaphids belong to different genera, indicated the Iapetus Ocean remained wide enough to act as a barrier to migration for these shallow water continental-shelf forms. In the cooler waters of Gondwanaland are found the *Selenopeltis* and Hungaiid-Calymenid faunal provinces, including trilobites of the family Hungaiidae, Calymeniidea, Pliomeridae, Illaenidae, and endemic Asaphidae. The differences between Bathyurid fauna and Hungaiid-Calymenid faunal provinces was due to a combination of climate factors and geographical separation.

The same biogeographical distribution seems to apply to articulate brachiopods as well. The Balto-Scandian region is better defined in the brachiopod then the trilobite faunas, and for much of the period can be considered a distinct biogeographical province.

In the later part of the Ordovician genera of families previously limited to one faunal province appear in another, indicating a tendency towards migration and cosmopolitism. Changed in oceanic circulation (distribution of planktonic larvae etc) along with approaching continental masses would have made possible migrations of shallow water benthos.

Intelligence

The tremendous evolutionary radiation of nautiloid cephalopods meant an increase in the level of consciousness in Paleozoic oceans. Cephalopods are the most intelligent of all invertebrates, owing to the development of elaborate manipulative organs (tentacles for touching and grasping). One researcher described the common octopus as like a sort of aquatic dog or cat. Although Ordovician cephalopods were probably not equal to modern forms in intelligence, they were certainly superior to that of contemporary (non-cephalopod) life-forms.

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last modified ATW040318
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The Early Ordovician

The Early Ordovician Epoch: 488 to 472 million years ago

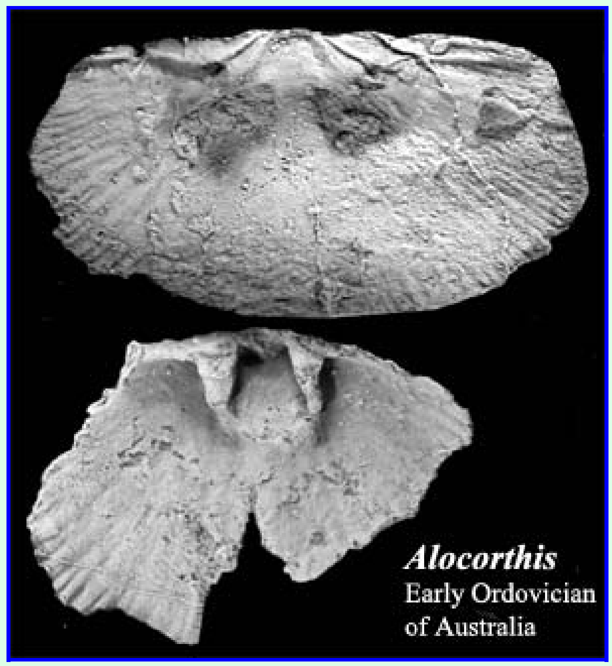
From the point of view of a hypothetical Late Ordovician oberver, the Early Ordovician was the "good old days." Things were simpler then. It was really just an extension of the Cambrian, but with a new generation of trilobites -- sleeker, probably a bit stronger, but still trilobites. Lots of phylogenetic change was in the air, or actually in the water, but it was mostly happening in the same lush, warm epicontinental seas. Besides, organisms stuck to their roots back then. There were crinoids from Baltica and other crinoids from Laurentia, and yet others from East Gondwana, and you could really tell the difference. None of this messy business with everyone running around everywhere in a totally disorganized fashion. It all would have been just fine if it hadn't been for that worthless Taconic Orogeny. Everything was going along just great, but then Baltica and Laurentia got too close, and suddenly we've got mountains twelve thousand meters high sprouting like mushrooms overnight. Things went to hell pretty fast after that, I'd say.

As in the ramblings of many old-timers (such as ourselves), hypothetical or otherwise, there is both more and less here than meets the eye. Things really were simpler in the Early Ordovician. Metazoan diversity was on the edge of another leap almost comparable to the Cambrian explosion. However, this was a slower matter, and the long run results were mixed. The echinoderms are a good example. Crinoids had evolved well before the Early Ordovician. But during this epoch, they became dominant in many ecosystems on the continental shelves, a dominance they were destined to maintain into the Mid-Jurassic in some regions. Asteroids ("star fishes") and ophiuroids ("brittle stars") both evolved in the Early Ordovician. Asteroids didn't become important until the Cretaceous. Ophiuroids have never amounted to much. The Early Ordovician also saw the evolution of two new high-level taxa of blastoids -- but the entire clade was extinct by the end of the Ordovician. Other novelties of the Early Ordovician met similarly mixed fates, *e.g.*, several new types of articulate brachiopods (Strophomenida & Rhynchonellida) and planktonic graptolites.

Colcocoryphe: Early Ord. of Portugal

The world of the Early Ordovician was also much like the Cambrian. Stromatolites were still common. In fact, there had been a moderate resurgance of stromatolites in the Furongian. However, the Early Ordovician was the last epoch in which these massive bacterial colonies would be common. The renewed decline of stromatolites was simply more opportunity for sponges, bryozoans, and corals, who flourished by replacing stromatolites in the Early Ordovician. Similarly, bioturbation of near-shore sediments by annelid worms, bivalves, trilobites and other burrowing forms was not yet universal, and sea bottoms stiffened by algal mats were still relatively common. Again, the Early Ordovician was also probably the last epoch for which this was true.

The fauna of the Early Ordovician was also strongly endemic. In fact, sharp differences between local faunas continued well into the Middle Paleozoic. However, this feature of Paleozoic life was exaggerated in the Early Ordovician due to the wide dispersal of continental cratons in the temperate and equatorial zones. The exact position of many of the continents remains controversial, probably because of this dispersal. Its hard to tell, for example, precisely where Avalonia and Baltica were in the Early Ordovician, since they weren't in contact with any other land masses. Avalonia and Baltica lay to the south and east of Laurentia. Siberia was to the northeast. The are between them was the broad and loosely confined Iapetus Sea. Further east, poorly known microcontinents were assembling other bits and pieces of what would one day be Asia. Finally, yet further east, Australia and the Chinese terranes formed the tail end of East Gondwana. The rest of Gondwana lay far to the south, as a huge south polar continent. Since no land plants had yet evolved, and Ordovician climates were well stratified from north to south, this was a broad, lifeless barrier to dispersal, not the east-west faunal highway it would become in the Devonian and Late Paleozoic.

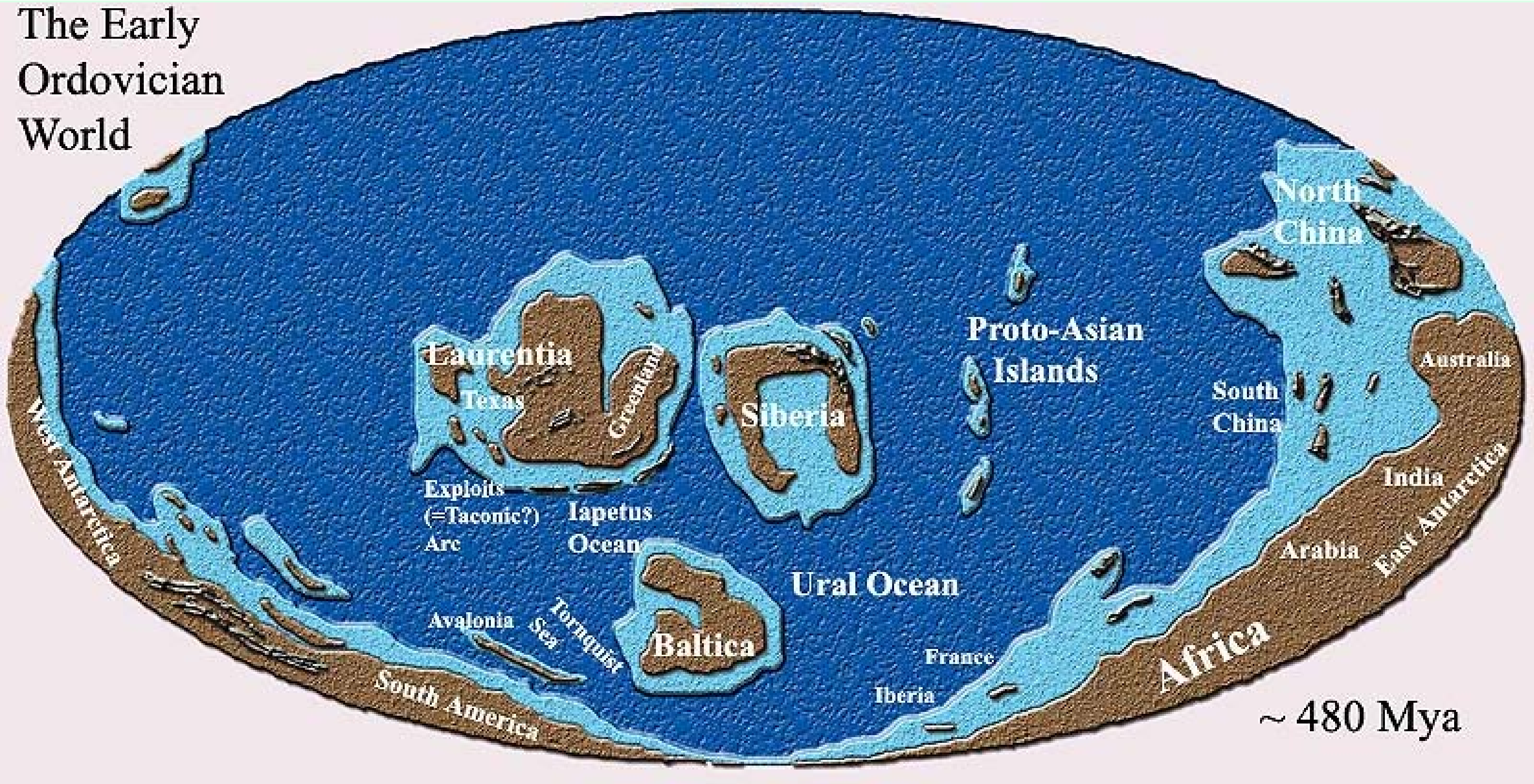


Alocorthis
Early Ordovician of Australia

Image credits: *Isograptus* from **Geological Society of Australia, Victoria Division.** *Colcocoryphe* from the **Paleontological Museum, University of Oslo**. *Alocorthis* from Paterson & Brock (2003).

ATW041125.

Early Ordovician Geography



This map is derived from several sources, including two different time slices from Jan Galonka, Dr. Ron Blakey's Paleogeographic Globes, the Paleomap project, and Mac Niocaill *et al*. (1997). We'd probably put Baltica a bit further east, if we were to do it over again. Note that Laurentia and Baltica are rotated about 90� clockwise from their present orientations.

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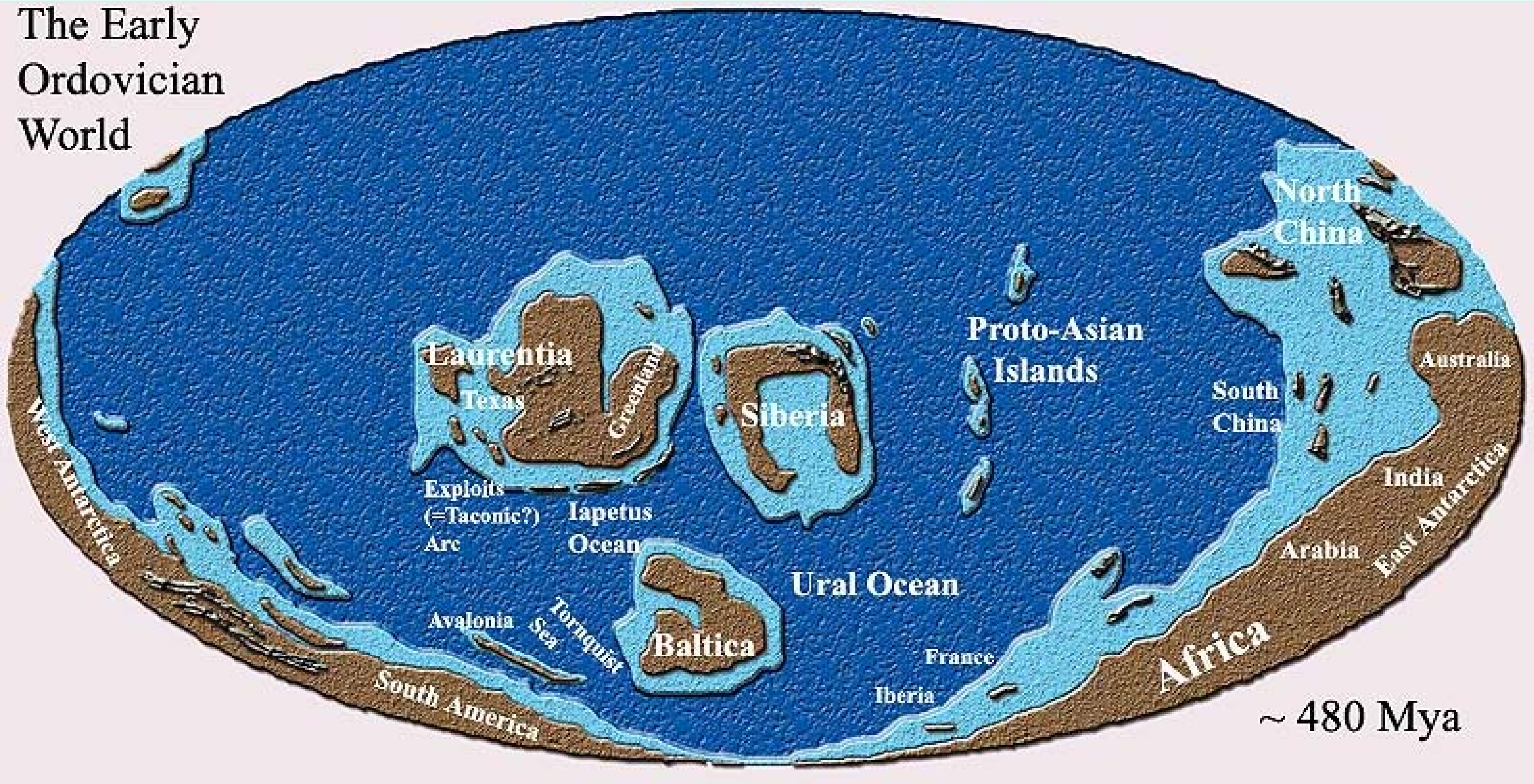
The Tremadoc

The Tremadocian Age of the Early Ordovician Epoch: 488 to 479 million years ago

As we have introduced the Early Ordovician world fairly extensively on theEarly Ordovician page, we will defer to that discussion by way of introduction.

Geography of the Tremadoc



This map is the same as that found on the Early Ordovician page. However, we thought that this would be a good place to talk about the perils of navigating the paleoseas. It might be a good idea to add some scrollwork and illuminated drawings with notices like "Here be dragons," the point being that some of these maps are only slightly better than those produced by medieval cartographers of the European tradition (compare a contemporary Chinese map). The University of Texas gives, as an example, a version from a 1472 edition of the **Etymologiae** of Isidorus (University of Texas Special Collections site). This is grossly unfair to both Isidorus and medieval (actually Rennaisance) Europeans. "Isidorus" was Bishop Isidore of Seville, who wrote in about 630. Much better maps were created by practical men of commerce in the Fifteenth Century, who certainly didn't rely on Seventh Century clerics for advice on navigation. But, back to our subject.

The Early Ordovician is particularly problematic because so many of the main landmasses were separated by ocean. In some cases, continental latitudes and orientations can be estimated from *paleomagnetic* data. However, relative longitude is usually established by looking at rock strata which were once shared with adjoining continents. *See* Dalziel (2005) for a non-technical example of how this is done. That analysis can't be performed if the continents are sparated by deep ocean. Worse, for continents near the equator, even good paleomagnetic data can be misleading, since, without knowing the orientation of the Earth's magnetic field, we can't be sure whether the latitude we calculate is North or South.

You'd think the last problem, in particular, would sort itself out. But compare the positions of Siberia on Jan Golonka's **Tremadoc map**, or the one reproduced at Jeff Poling's **Dinosauria site**, with the map from Chris Scotese's **Paleomap Project**. Plainly, Golonka and Scotese read the paleomagnetic data in opposite senses. That, in turn, affects the position of Greenland -- known to be close by -- which, in turn, causes the North American craton to be rotated to differing degrees. We, of course, fudged the issue and put Siberia squarely *on* the equator. **Ron Blakey's map** has partially dodged the issue by moving North America slightly further west, so its orientation isn't so closely coupled to the position of the Siberian terrane.

All of this interacts with the longitude of Baltica, which is unknown because it was not in contact with anything else. Blakey has Baltica in an easterly position, south of Siberia, as does Scotese. However, Golonka places Baltica further west. We followed Golonka; but, as suggested in a note to our map, we probably guessed wrong. One of the few constraints on Laurentia (North America) is that we can be certain that Avalonia, and other slices of western Gondwana, were peeling off Gondwana and hitting the Laurentian coast from Greenland all the way to Texas, beginning in about the Floian. MacNiocaill *et al*. (1997). That can't work if Baltica is in the way. Similarly, Iberia, France, and other *eastern* fragments of Gondwana were scheduled to dock with Baltica. So, all things considered, Baltica ought to be off to the east by a significant margin. Otherwise, the **Alhambra** ends up being built in **Tomsk**, where it would look somewhat out of place.

Marine Invertebrates

Phylum : **Sipunculata?**
Class: **Palaeoscolida**
Order:
Family:

Palaeoscolex piscatorum

Size:
Horizon: Tremodocian
Locality: England
Comments:
image from

Protocycloceras

?

Phylum : **Mollusca**
Class: **Cephalopoda**
Subclass: Palcephalopoda
Infraclass: unspecified
Order: **Ellesmerocerida**
Family: Protocycloceratidae

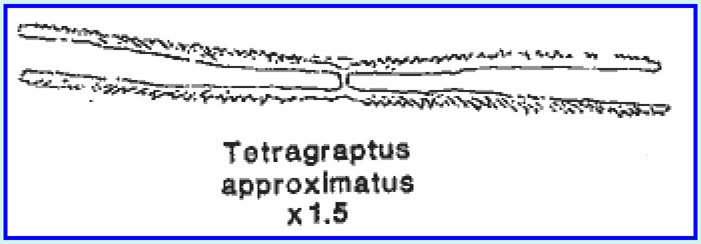
Protocycloceras sp.

Size: Length about 9 cm
Horizon: Tremadoc
Distribution: Laurentia (USA)
Comments: image from Teichert 1988

The Floian (Early Arenig)

The Floian Age of the Early Ordovician Epoch: 479 to 472 million years ago

Credits: Thanks to Andreas Johansson for correcting some errors in Swedish spelling and word-use.

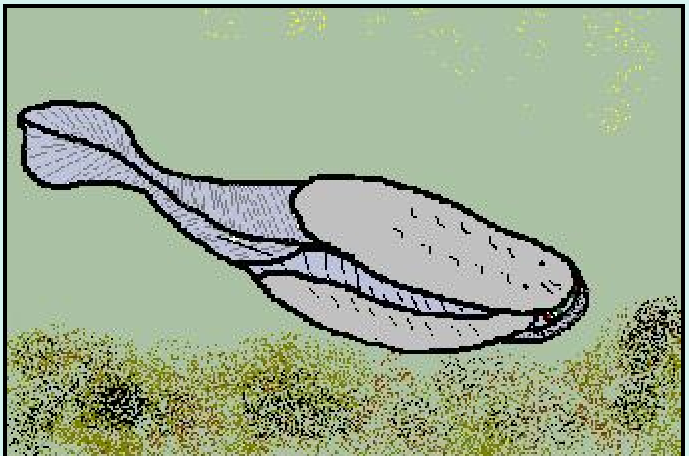


The second half of the Early Ordovician is now named the Floian. In Britain and various other systems, it was previously known as the Arenig, from the Welsh locality of that name. The Arenig was part of the original Ordovician System, and so it had a strong claim to historical priority. Moreover, everyone agreed on the stratigraphic level at which the Arenig began -- with the appearance of an easily-recognized group of graptolites. The problems were at the other end. First, careful dating showed that the Arenig, as that stage name had been used in Britain, lasted well into Middle Ordovician. Second, in other locations, the Arenig referred to a stage with a different end-point. Finally, even this general agreement had no close parallels in the North American or Western European systems, both of which have nothing comparable to the Arenig.

Consequently, the ICS chose to start over again. Although we are unhappy with that choice, the reasoning is so sound that we are forced to follow the logic of it. The problem is that there is almost nothing like the **sound of Welsh**. It is one of a handful of languages that are inherently good to hear, even without understanding. And, as peculiar as it may seem, one of the great attractions of geology has always been the romance of its place names. Admit it. Would you really have developed an interest in the subject without names like *East Gondwana*, the *Old Red Continent*, the

Maotianshan Shale, the *Tethys Seaway*, or the *Deccan Traps*? In the long run, the poetry of the Ordovician stage designations (some of the very first geological ages to be given names) has been more important to geology than the meaningless fourth decimal place of their radiometric dates. But the ICS has no poets, and so the *Arenig*, *Llanvirn*, *Llandeilo*, and *Caradoc* are all gone -- replaced by stratigraphic elevator music, like the names of suburban subdivisions or of clinics which cater to the more fashionable mental disorders.

However, rather than burst into an aggressive rendition of ***Men of Harlech***, we will go with the flow -- literally in this case, as the base of the Floian is the first occurrence of the graptolite *Tetragraptus approximatus* in the Diabasbrottet (= "diabase quarry"), located near the **town of Flo**, about 15 km east of Trollhättan, in southwest Sweden **[2]**. Bergstrom *et al*. (2004). The quarry is actually located on "Mount" Hunneberg, one of two flat-topped hills famous for their particularly dense population of moose -- although, in our experience, moose tend to be rather dense just about anywhere.



Generalized arandaspid

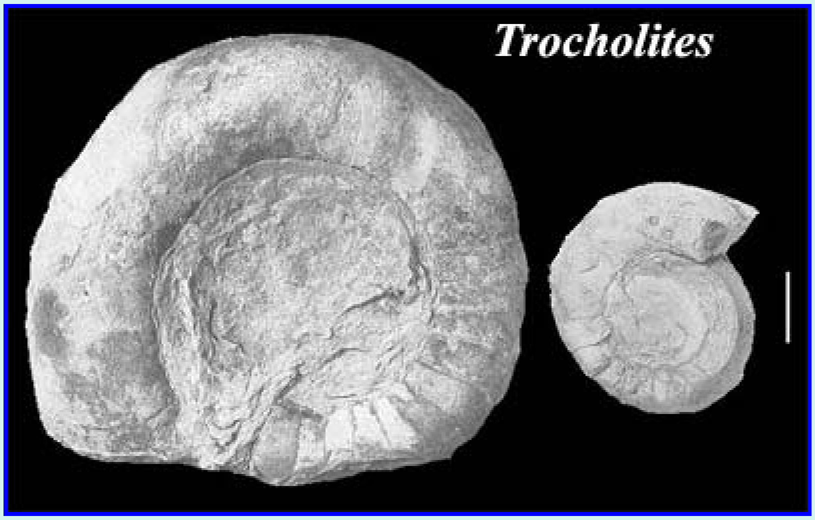
The Floian began with a rapid rise in sea level (a "marine transgression") world-wide. For this reason, the bottom of the Floian is often quite easy to find. If one locates a place of approximately the right age, where terrestrial or wind-scoured deposits have been overlain with marine sediments containing the distinctive *Tetragraptus*, chances are very good that you have located the base of the Floian.

This transgression was peculiar in that it is associated with a strong, negative d^{13}C excursion of 2‰ and, at least in North America, the deposition of a thin micritic layer. Nice jargon, but what does it mean? Carbon has two stable isotopes, ^{12}C and ^{13}C, with the latter having one extra neutron in the nucleus. In theory, one neutron more or less should make absolutely no difference to the chemical behavior of the carbon atom. In practice, this is almost true, but not *quite*. Photosynthesis by plants and "blue-green algae" (photosynthetic bacteria) incorporates atmospheric CO_2 into sugars. For obscure reasons, photosynthesis tends to pick up a slightly larger fraction of light carbon (^{12}C) than it "should" by chance alone. Biological reactions can tie up immense amounts of carbon. When lots of atmospheric carbon gets tied up in biological products and is not recycled -- which can happen for a variety of reasons -- the isotope ratio in the atmosphere gets skewed toward the "heavy" ^{13}C isotope. So, photosynthetic organisms living at that time pick up a greater than normal fraction of ^{13}C. That's called a *positive* d^{13}C excursion and can be detected in fossils by isotope analysis. The opposite, a *negative* excursion, happens when lots of stored biological carbon is suddenly recycled, such as by the burning of fossil fuels.

So why do we see a strong negative excursion at the base of the Arenig? We can be reasonably sure that Ordovician brachiopods did not drive SUVs. One of the many advantages of being sessile is the elimination of all traffic congestion. The clue may be the "micritic layer." This betokens biofilms formed by sulfate reducing bacteria. These bacteria normally work in tandem with methane-eating bacteria, like so:

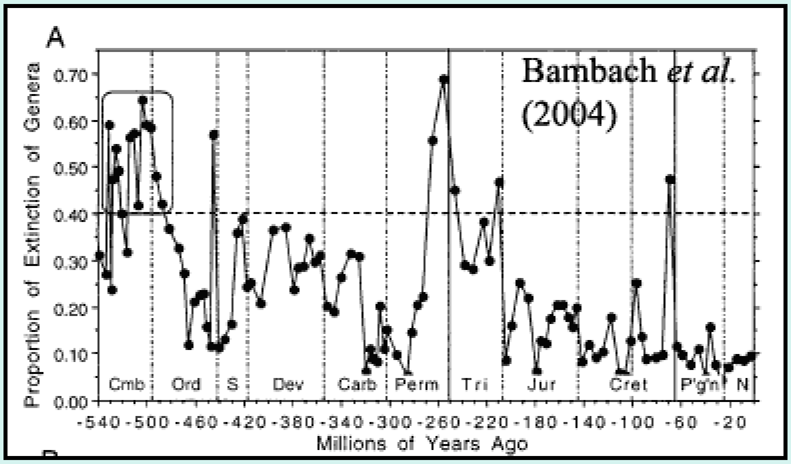
$CH_4 + 2\,H_2O \Longrightarrow CO_2 + 4\,H_2$ methane oxidized to carbon dioxide and hydrogen gas

$SO_4^{2-} + 4\,H_2 + H^+ \Longrightarrow HS^- + 4\,H_2O$ sulfate reduced to sulfide and water



This reaction is sometimes driven by iron II (Fe^{2+}), which not only catalyzes some the key steps, but tends to remove the sulfide at the end as insoluble FeS (pyrite). Schouten *et al*. (2003); Madigan *et al*. (2003).

The key fact here is that natural releases of methane tend to be *very* "light." An increase in atmospheric methane would dilute the "heavy" carbon in the atmosphere after the methane was converted to carbon dioxide by these bacteria. So the entire mystery may be solved by invoking methane release, probably associated with the sea floor spreading ridges which presumably created the sea level rise in the first place. This is all quite similar to the developing picture of certain events in the Aptian-Albian epoch of Cretaceous time.



The Floian has recently been identified as a statistical breakpoint for metazoan evolution. Bambach *et al*. (2004). Prior to the Floian, genus-level turnover was extraordinarily high, and the entire metazoan tree looks unstable, with large taxa frequently experiencing random-looking booms and busts. During the Floian and Middle Ordovician, extinction rates dropped sharply and remained far lower than in Cambrian and Tremadoc times; and they remained lower, except for the three actual mass extinctions of Phanerozoic time. These generalizations depend on a kind of data that may rightly be viewed with some suspicion. However, the trend line seems safe enough. Whatever genus one might be, one's life expectancy began to go up dramatically over the Floian.

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The Middle Ordovician

The Middle Ordovician Epoch of the Ordovician Period: 472 to 461 million years ago

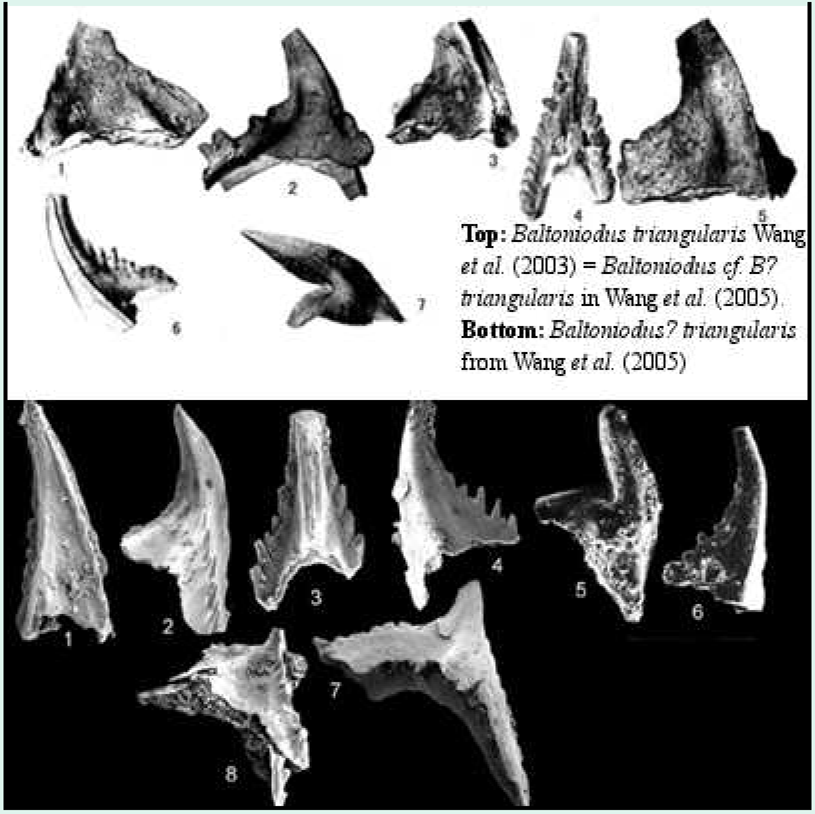
Introduction

The Middle Ordovician includes the Dapingian (Middle Arenig) and Darriwilian (Late Arenig, Llanvirn and Llandeilo) Ages. Historically, it has been the most difficult and contentious boundary in the Ordovician. The Ordovician conveniently left us good records of both graptolites and conodonts, as well as trilobites, brachiopods, and some stable isotope excursions. Unfortunately, the non-Gondwanan continents were scattered and fragmented during much of the period. As a result, the fauna of one continent often had little or no overlap with the fauna of another, making correlation extremely difficult. This is particularly hard luck because the precise stratigraphy of the Middle Ordovician lies at the core of a key issue. As we will see, a completely unreasonable number of important clades first appeared in this epoch, during what has been called the "Great Ordovician Biodiversity Event." This event was the mirror image of a mass extinction, and paleontologists are naturally anxious to understand precisely when, and under what conditions, such an unusual radiation might have occurred.

Special Credit: Thanks to Prof. Stan Finney for responding to a conodont issue. We rewrote the stratigraphic problem considerably after receiving his explanation. ATW080307.

Stratigraphy: the Middle? *c.f.* Ordovician

The base of the Middle Ordovician is the most difficult stratigraphic problem we have looked at thus far. Eventually, after some false starts, the ICS selected, as the Middle Ordovician global stratotype section and point, the Huanghuachang Section, an exposure of the lower Dawan Formation near **Yichang**, in Hubei Province. Wang *et al.* (2005). This lies in Central China, near the **Yangtze River**, and -- by no coincidence at all – just a few km up the road from the GSSP for the Hirnantian Age of the Late Ordovician. Oddly, the Huanghuachang Section lacks a good set of graptolite index fossils. This is unfortunate for an Ordovician GSSP, since so much Ordovician stratigraphy has been done using graptolites. However, there are at least a few graptolite markers, and a number of other index fossils are present.



Top: *Baltoniodus triangularis* Wang *et al.* (2003) = *Baltoniodus cf. B? triangularis* in Wang *et al.* (2005). **Bottom:** *Baltoniodus? triangularis* from Wang *et al.* (2005)

The original guide event for the Middle Ordovician was supposed to be the first appearance of the conodont *Tripodus laevis* on the theory that *T. laevis* would permit correlation with Ordovician conodont zones in Northern Europe, Newfoundland, the Western U.S., and elsewhere. Unfortunately, for reasons too complicated to get into here, *T. laevis* has been described under at least four different names, including *Acodus combsi*, *Scolopodus alatus*, and *Tripodus combsi*. In the profoundly understated words of Bergstr�m & Albanesi (2001), "the fact that different authors use a different species designation for the same biozonal index species is likely to cause confusion not only among non-conodont workers." To make matters worse, someone pointed out -- during an ICS field trip to a proposed GSSP, no less -- that *T. laevis* seemed to appear at different levels even within related exposures in Nevada. Thus, when Wang *et al*. (2003) proposed using another conodont, *Baltoniodus triangularis* **[5]**, and the well-sampled Chinese section at Huanghuachang, the idea was well-received. Even better, the *lowest B. triangularis* level coincided almost exactly with the appearance of *T. laevis*, which was also present in this section.

But the Middle Ordovician seems to be cursed. We suspect that this is the evil work of a secret cabal of immortal druids, justly enraged at the abandonment of the old Welsh names for the Ordovician stages. Whatever the ultimate cause, further investigation showed that the fossils described as *Baltoniodus triangularis* at Huanghuachang, were in fact two different, overlapping species, neither one of which was actually *Baltoniodus triangularis*. Indeed, neither species had ever been properly described or named. In the iconography of stratigraphy, these are referred to as *Baltoniodus? triangularis* and *Baltoniodus? cf. B? triangularis*. We may refer to the original conodont and its two *doppelgangers* as Bt, B?t, and B??t.

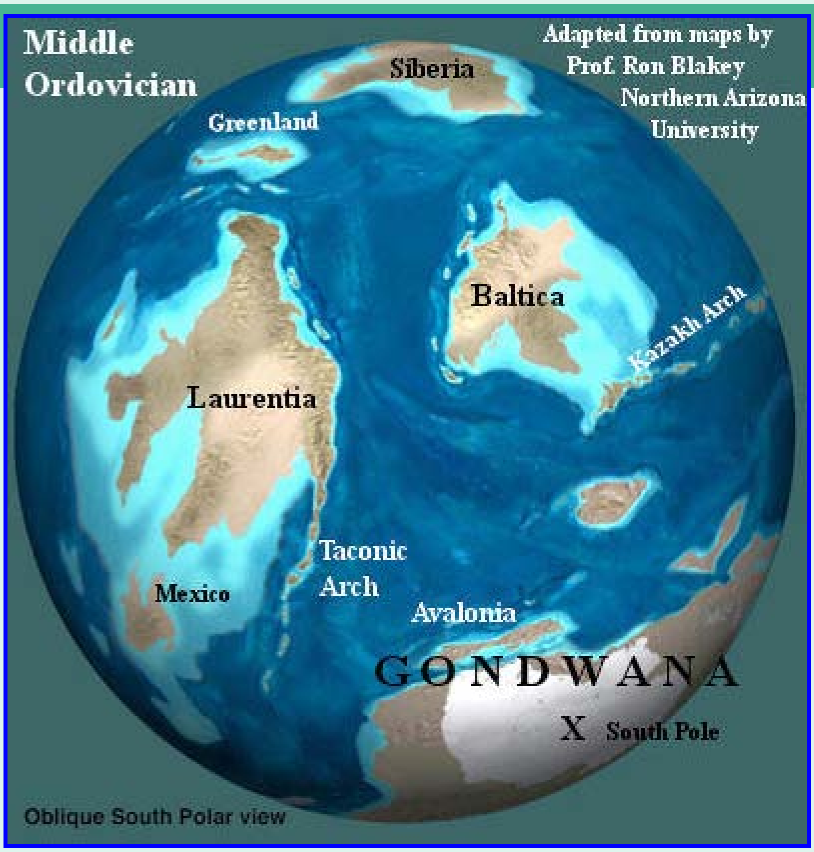
This problem was not confined to Huanghuachang. As we understand the facts, many of the European Bt zones turned out to be B?t or overlapping bands of Bt and B?t. Unfortunately, the conodont which defined the proposed Huanghuachang GSSP was neither Bt nor B?t, but B??t -- a species apparently unique to the Dawan Formation and thus utterly useless for correlation.

One can only imagine the state of mind of the Ordovician Subcommission, as the members watched 20 years of hard work start to go up in smoke. Fortunately, somone with a very practical turn of mind realized that by deftly moving the proposed GSSP up-section a few meters, it could be made to coincide with the first appearance of **B?t**, which would then correlate with the numerous wrongly named, but correctly mapped, European sections.

Thus, in Wang *et al.* (2005), the base of the Middle Ordovician was elevated about six meters from its position in Wang *et al.* (2003) and a question mark was inserted to redefine the level as the earliest appearance of conodont *Baltoniodus? triangularis* -- not to be confused with *Baltoniodus triangularis* (*sensu* Wang *et al*., 2003), also known as *Baltoniodus? cf. B? triangularis* (*sensu* Wang *et al.*, 2005). A few problems were created by the last-minute change from Bt to B?t. For example, the authors state that, "This [B?t] level is similar to that proposed by Webby (1994, 1998) as a boundary marker and coincides with the base of the *Tripodus laevis*." Wang *et al.* (2005: 106). Unfortunately, this is no longer true, as their figures correctly show. See Wang *et al.* (2005: 107, fig 3).

We are tempted to refer to this epoch as the "Middle? *c.f.* Ordovician." But this would be more than a little unfair, given the myriad of stratigraphic blowouts and pot-holes succesfully traversed on the way to the Huanghuachang GSSP. Even if we now have a Middle Ordovician GSSP which is slightly ambiguous, we are very much better off than the we were as recently as the 1990's. If there turn out to be real, as well as theoretical, problems with the GSSP, they will come to light soon enough, and the matter can be corrected. ATW080215; rev'd ATW080307.

Geography



As mentioned, the Middle Ordovician saw the continents scattered. The East coast of Laurentia (North America) would eventually be augmented by two successive waves of refugees from Gondwana, Avalonia and Armorica. However, both were still well-separated from Laurentia during the Middle Ordovician, as were various future parts of southern Baltica (Europe), which also derived from Gondwana. Siberia, Greenland, and Kazakh likewise had little connection to any other landmass. Cocks & Torsvik (2002). The positions and connections of the Chinese and Southeast Asian terranes are even less well understood. They may well have been widely scattered to the east of Baltica, as in the reconstruction by Cocks & Torsvik. However, Australia was probably secured to the main mass of Gondwana (Africa, India, South America, and both Antarcticas) around the South Pole, which was located in today's West Africa.

We should note two disagreements we have with Prof. Blakey's map. First, he shows a south polar ice cap. We do not know what the evidence is for this detail. Several groups have found no evidence of glacial conditions in North Africa at this time. See the discussion of Ordovician climate for more information on the possibility of ice sheets in the Ordovician. Second, the current information on Siberia places it south of the equator, probably due west of Baltica, during the Middle Ordovician.

Because the continents were well-separated, the animals who lived in the shallow waters around them tended to be endemic. That is, the conodonts, mollusks, trilobites, etc. of one continent had little or no genetic contact with those of any other. This makes life difficult for stratigraphers, but also may have furnished more natural laboratories for the "experiments" of evolutionary chance. It also increased the amount of shallow water available for animal life -- and shallow waters were the only environment in which animals lived at this time. ATW080215; rev'd 080311.

Life in the Sea

One of the defining characteristics of almost all geological epochs is the nature of its reefs. However, during the ~50 My preceding the Middle Ordovician, there had been almost no reefs of any kind. The Middle Ordovician marks the return of the entire reef biome. Stanley (1998).

Like a great deal of Middle Ordovician life, these reefs were a mixture of forms, some old and some very new. These reefs were not extensive, and many were no more than new varieties of bacterial stromatolites reinforced with sponges and calcifying red algae (see image). To

these were added crinoids, which had probably first evolved in the Middle Cambrian, as well as tabulate corals and bryozoans, who were Early Ordovician newcomers. However, the Middle Ordovician also saw the development of the first massive stromatoporoid sponges and rugose corals, which together set the pattern for the next 100 or 200 My (depending on exactly how one defines "the pattern"). Benton & Harper (1997); Webby (2004).

As mentioned above, the nearshore, and specifically the nearshore sea bottom, was probably the only environment which supported animal life at the beginning of the Middle Ordovician. That was no longer true at the end of the epoch. First, animals began to colonize deepwater marine environments, as shown by the presence of graptolites and of trace fossils. Hagadorn (1998) (citing work of SC Finney and others).

Leoniorthis, an articulate brachiopod from the Middle Ordovician of Russia. Egerquist (2003).

Second, open water, planktonic life began to be an important part of animal ecospace. Peterson (2005) argues that animals developed large, floating, yolk-filled eggs several times by the end of the Cambrian. This allowed embryos to disperse more widely, as they could float for longer periods, feeding on yolk before settling to the bottom. By the Middle Ordovician, this pelagic picnic was being harvested by the planktivores, such as the feeding larvae of the polychaete worms *Nereis* and *Chaetopterus*. *Id.*

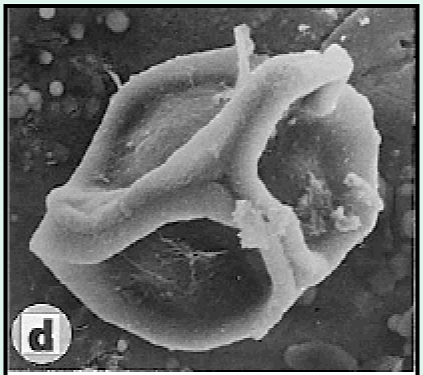
Toward the end of the epoch comes the event for which the Middle Ordovician is really well known, the great surge in metazoan diversity of the Darriwilian. This Ordovician "explosion" is best known from the articulate brachiopods, because of their excellent fossil record, and particularly the rhynchonellids. Stanley (1998); Cocks & Torsvik (2003). The most spectacular radiation of the age was among cephalopod mollusks. Several new orders radiated or appeared for the first time in the Middle Ordovician, including the Endocerida, Ellesmerocerida, and the nautiloid Tarphycerina.

Equally important are very early vertebrate remains. Several different vertebrate types seem to have lived at this time. So, for example, isolated fragments of some arandaspid-like fishes from the **Amadeus Basin** in Australia and from Bolivia. Janvier (1996). In the last few years, new Ordovician thelodonts have also been recovered in arctic Canada, some of which may be of Darriwilian age. Sansom & Elliott (2002). Possible chondrichthyan scales have been found in the Harding Sandstone of the western United States (Sansom *et al*., 1996) together with *Astraspis* and the unclassifiable *Eriptychius* (Halstead, 1973).

The significance of these particular remains is that they show the development of all but one of the principal types of vertebrate mineralized tissues at a rather early date. Janvier (1996). On theoretical grounds, some writers have proposed that this correlates with an (equally theoretical) large-scale gene duplication event. (There is no question that many chordate regulatory genes were duplicated, but it is less clear whether this was an "event" or a long series of individual duplications). ATW080215.

Image credit: from **D&D Fossils & Meteorites**.

Life on Land



Tetrahedraletes medinensis spore. Photo by WA Taylor. from Kenrick & Crane (1997).

This is the first epoch for which it is meaningful to add this heading. Thereis little doubt that plant life had, at last, crept onto the margins of the land by this time. In fact, the earliest confirmed plant fossils may be a bit older, from the later Floian. They consist of the spores of a liverwort-type plant some 476 My old. Shaw & Renzaglia (2004). The understanding that they are true land plants is derived from the co-occurrence of a decay-resistant wall and tetrahedral form which, together, are diagnostic of land plants. Kenrick & Crane (1997).

Fossilized fungal hyphae have also been recovered from the latest Darriwilian of Wisconsin, USA. The indications are that these were mycorrhizal fungi: symbiotic fungi which serve as, or are associated with, plant roots. Redecker *et al*. (2000). This is an important step. It suggests that, by the end of the epoch, plants were growing in regions where they were not covered with water, and therefore required a method of extracting minerals from the soil, at least for substantial periods of time. Thus, by the end of the Middle Ordovician, a hypothetical observer in space might well have seen the beginnings of a pale green fuzz along river valleys and flood plains, far from open water. ATW080215.

ATW080215.
Last revised ATW080311

Dapingian (Middle Arenig): 1

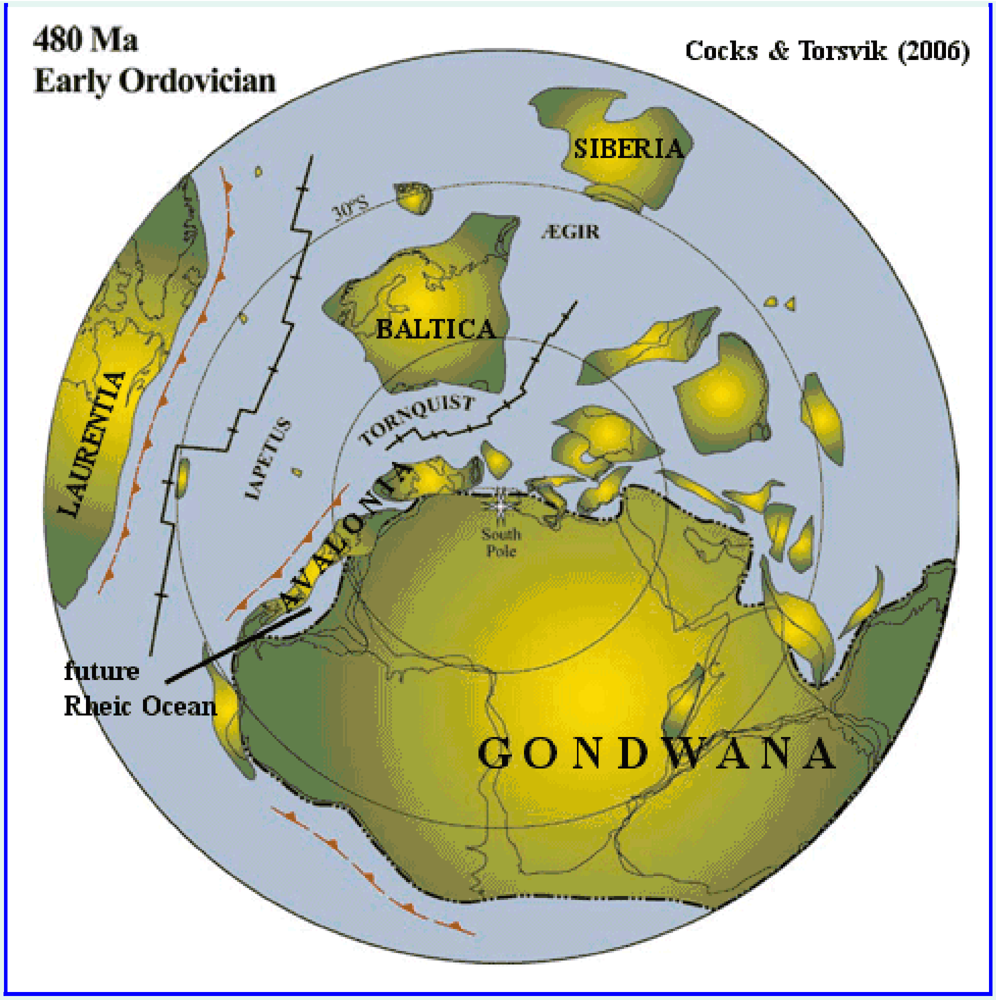
The Dapingian Age of the Middle Ordovician Epoch: 472 to 468 million years ago

Introduction

The Dapingian was a sort of dry run for the Darriwilian and the Great Ordovician Biodiversity Event ("GOBE"). The name of the Dapingian Age, like its global stratotype section, is a little dicey. *Daping* is the former name of a similar section (and also of a small city) in the Yangtze Gorge area. Wang *et al*. (2005). Yet Western readers, at least, should be properly grateful that this slice of the Ordovician was not named the "Huanghuachangian" after the actual type section.

Geography

Prior to the Dapingian, it is not entirely clear where Baltica (Scandinavia + European Russia) was. Cocks & Torsvik (2005). Baltica seems to have been drifting in a generally west-southwesterly direction during most of the Proterozoic. At some point, as Nawrocki & Poprawa (2006) describe



it, Baltica hit the tectonic equivalent of a brick wall to the south, near the Gondwanan landmass. The craton effectively bounced, abruptly changing direction to north-northwest and rotating counter-clockwise about 55°. This rotation was completed during the Dapingian, and Baltica was redirected NNW, on a collision course with Laurentia (North America).

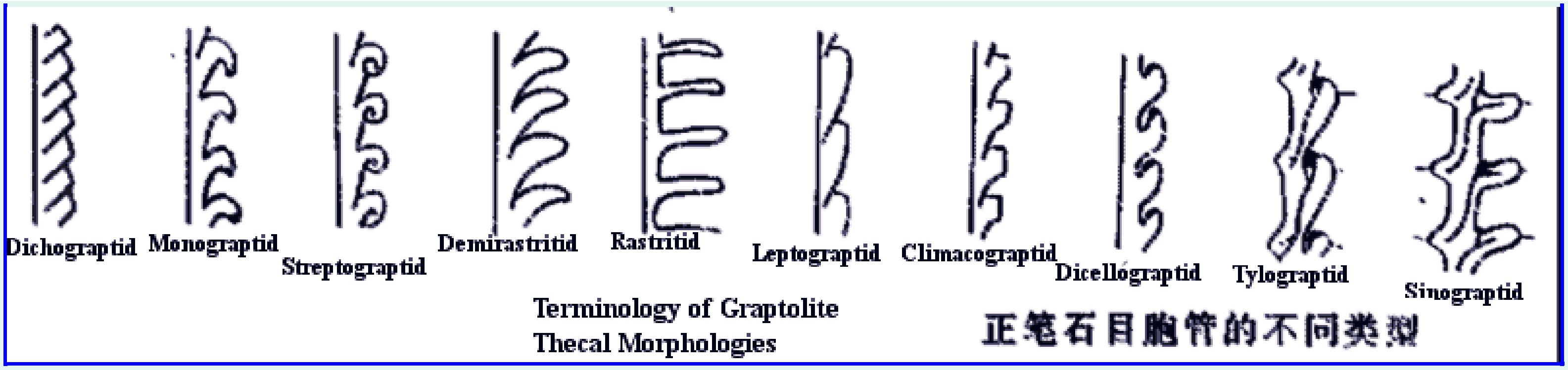
Also during the Dapingian, somewhat west of Baltica, a string of small blocks crumbled off the northern edge of Gondwana and began slowly moving north. These were the Avalonian terranes, which later accreted onto the east coast of Laurentia and the south coast of Baltica, forming "the Maritime Provinces of Canada, Newfoundland, southeastern Ireland, southern Britain, and a substantial area of Europe surrounding Belgium." Cocks & Torsvik (2005). The slowly shrinking gap between Western Avalonia and Laurentia is often referred to as the Iapetus Ocean, while the corresponding waters between Eastern Avalonia and Baltica formed the Tornquist Ocean. The new basin between Avalonia and Gondwana became the Rheic Ocean. It also seems increasingly likely that similar small blocks were being stripped off Gondwana further east, at about the same time. These included parts of Germany and Italy, Greece, and the Czech Republic (= Perunica = Bohemia). Cocks & Torsvik (2002, 2006). However, France refused to join the rest of Europe, much less North America, although its traditional connections with Africa were becoming increasingly strained. Evidently, some things never change **[4]**. Nysæther *et al*. (2002).

Laurentia, and most of the other terranes outside Gondwana (Siberia and other pieces of central and northern Asia), were drifting slowly northward into positions around the equator. However, during the Dapingian, none of these lands was significantly north of the equator, with the possible exception of some Mongolian fragments. The South Pole was located in Algeria, and the core West (actually south, in that era) Gondwanan cratons of South America, Africa, Arabia, and India extended northwards on the opposite side of the earth from Laurentia, Avalonia and Baltica. East (then, north) Gondwana formed a massive tail, arching northwest from this core, reaching well north of the equator. Cocks & Torsvik (2006, 2007).

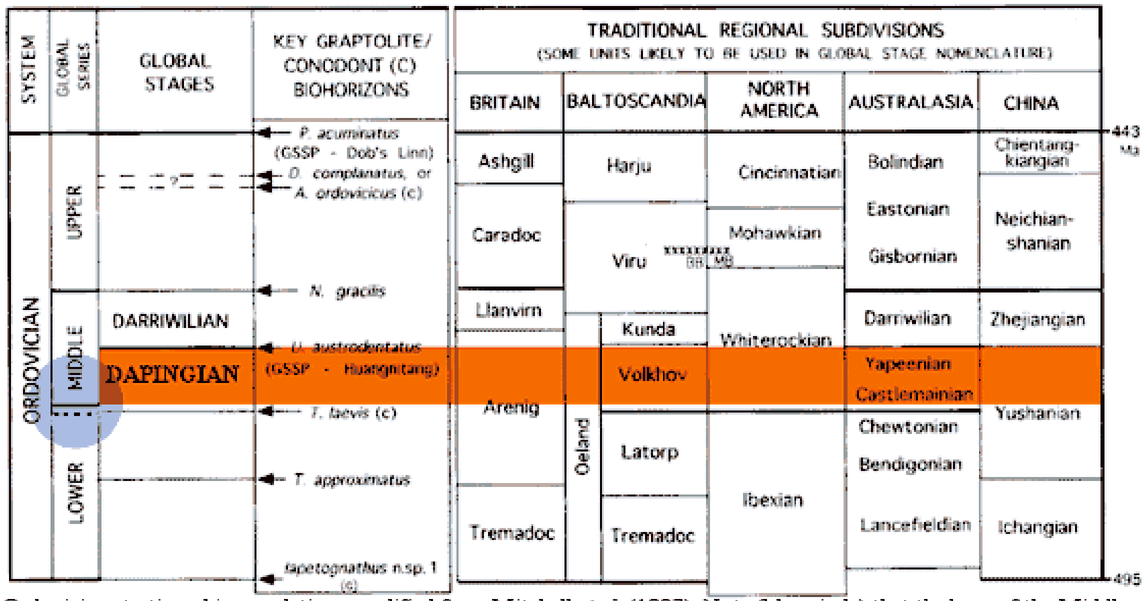
The Dapingian is bracketed by two pulses of rising sea level, without a strong intervening decline. Ghienne et al (2007). The Ghienne paper reflects careful interpretation along a roughly NW/SE transect starting from the coast of Algeria – thus covering an area very close to the Dapingian South Pole. The authors find no evidence of ice accumulation until the end-Ordovician.

Meanwhile, in the depths of outer space, a very large chondritic body in the Asteroid Belt seems to have been totally disrupted, resulting in a hailstorm of meteoric impacts toward the end of the Dapingian. It has recently been argued that this triggered the GOBE. Schmitz *et al*. (2008). The mechanism is unclear. ATW080223.

Stratigraphy



The Dapingian corresponds generally with Middle to Late Arenig of Britain, the Volkhov of Baltica, the Early Whiterockian of North America, the Castlemanian of Australia, and the Late Yushanian of China. It lies slightly above the *Tripodus laevis* conodont zone which, in turn is slightly above the first appearance of dichograptid graptolites (Benton & Harper, 1997), within the *Azygograptus suecicus* biozone.



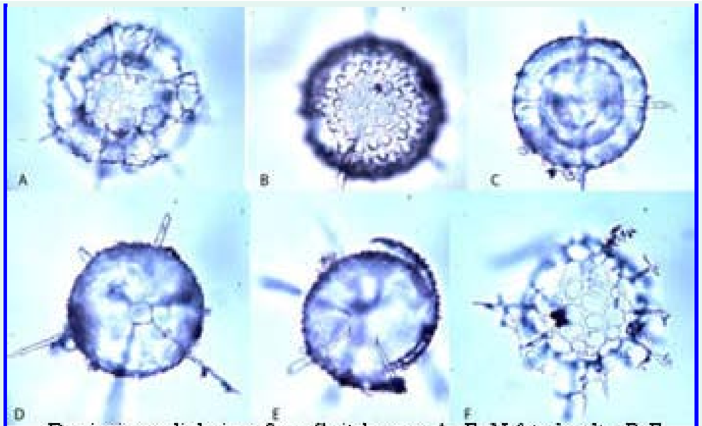
Ordovician stratigraphic correlations modified from Mitchell *et al.* (1997). Note (blue circle) that the base of the Middle Ordovician has been moved up, as the adopted GSSP lies slightly above the *T. laevis* zone.

No, we had no idea what all that meant, either. But, unlike you, we looked it up. A useful table of graptolite theca morphologies, lifted from the **China University of Geosciences site**, is reproduced above. According to Zhang & Chen (2003), the *A. suecicus* biozone "is defined by the FAD [first appearance date] of the zonal species [*A. suecicus*] which has proved to be rather common in both the Yangtze region and Jiangnan Slope regions, as well as in Scandinavia and Britain. However, the equivalent interval in Australasia and in the Zhujiang region of South China is characterized by the occurrence of isograptids and allied groups." Their **Figure 2(B)** shows a rough sketch of the infamous *A. suecicus* itself, as well as its isograptid sisters, cousins, aunts, etc.

We will move on, as we are unequal to the daunting task of making this material sound interesting. This is a pity, since it has many redeeming features. At this level, stratigraphy is perhaps best understood as a four-dimensional jigsaw puzzle the size of a planet, with billions of pieces. It is intimidating, tedious, frustrating -- but somewhat addictive. ATW080224, rev'd ATW080305.

Dapingian Life

The Dapingian saw a very modest radiation of animal life. The importance of the Dapingian radiations was not their size, or even novelty, but the selectivity of the groups which were diversifying. The Early Ordovician radiations equally affected the older Cambrian fauna and the new groups which had arrived at the end of the Cambrian and earliest Ordovician. The Dapingian saw (a) the *replacement* of the Cambrian fauna by a Mid-Paleozoic biota and (b) the radiation of the same taxa into specialized forms capable of invading level-bottom shelf and open pelagic communities,

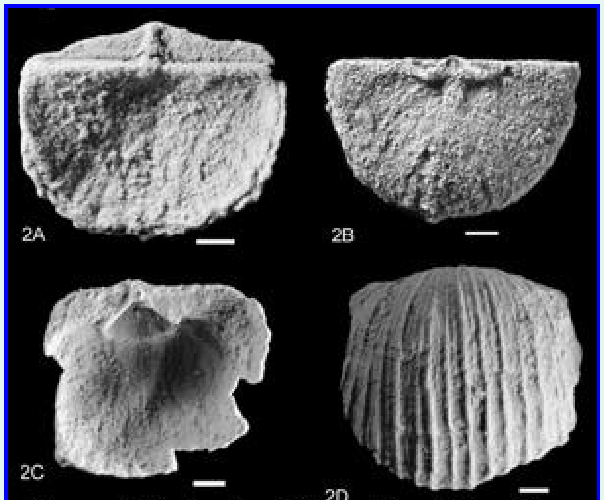


Dapingian radiolarians from Spitsbergen. A, F. *Nyfrieslandia*. B-E. *Antygopora*. Photo by, and from the website of, Prof. Jörg Maletz, State Univ.of N.Y. at Buffalo.

ecosystems which had not previously had an animal component.

These changes were particularly marked (or at least well-known) in the shallow seas covering the **Great Basin** of Western Laurentia (Nevada, Utah, Arizona). Shell beds came to be dominated by brachiopods and ostracodes, rather than trilobite exoskeletons. Pelagic radiolarians diversified and developed one or (as with many extant forms) more spherical shells, along with the pelagic graptolites. Conodonts and graptolites also made notable gains. Webby (2004a). Encrusting bryozoans and crinoids became more common on hard substrates. Taylor & Wilson (2003). ATW080229

Slugs > Bugs (Lophotrochozoa)



Unnamed plectambonitoid brachiopod from the Middle Ordovician of Estonia. Egerquist (2004). Scale bar = 1 mm.

Brachiopods seem to have led the way, replacing some of the benthic trilobite clades. Schmitz *et al*. (2008). Strophomenoids, particularly the plectambonitoids, were quite successful (Cocks & Torsvik, 2005), but linguliform brachiopods began a slow decline (Webby, 2004a). Stonolaemate bryozoans built gradually on the foundation they had laid in the Early Ordovician. Benton & Harper (1997).

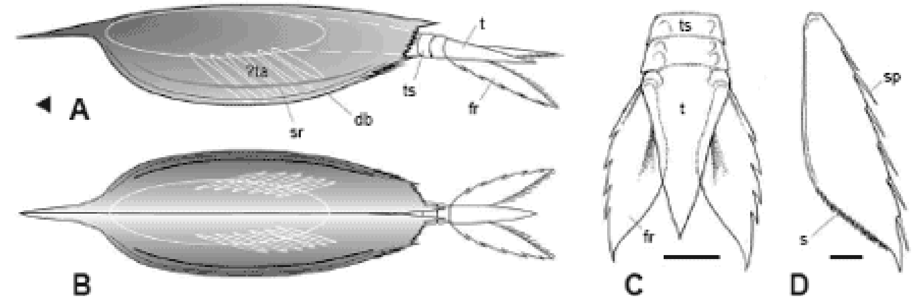
Among mollusks, the explosion of nautiloids occurred in the Darriwilian, but the higher level taxa had diverged by the end of the Dapingian. These may have evolved as endemic forms, but all responding to some selection for greater buoyancy control. Frey *et al*. (2004); Kröger (2004); Webby (2004a). By contrast, other mollusk groups found the Dapingian less congenial. In the gastropod lineage, the pre-gastropod bellerophontids made little headway. The Euomphalida and Macluritoidea radiated in the earlier Dapingian, but were already in decline by the end of the age. Bivalves had a small radiation, but the rostroconchs began to slide toward their extinction at the end of the Ordovician. Webby (2004a).

On the rare occasions when we are forced to comment on the state of the annelids, we usually occupy the space with complaints about the poverty of the fossil record. We have recently learned that machaeridians are armored annelids, so we may have to mend our ways. Vinther *et al*. (2008); *see* Christopher Taylor's (2008) **Catalogue of Organisms- Yay, Machaeridians!**, with citations and absolutely gorgeous illustrations therein. These worms first become common in the Dapingian. Webby (2004a). ATW080229

Bugs > Slugs (Ecdysozoa or whatever)

We generally have reasonably good information on the arthropods; but, for whatever reason, we've come up short this time. As stated above, the trilobites lost their numerical

Morphology of generalized caryocaridid. Vannier *et al*. (2003).



dominance of shell beds in the Dapingian. However, many trilobite groups (e.g. nileids, olenids) thrived in the Dapingian, often as specialized and endemic elements of the fauna. Benton & Harper (1997); Webby (2004a); Cocks & Torsvik (2005). In addition to the brachiopods, new groups of ostracodes, characterized by bearing two lateral crests in adulthood, multiplied among the benthic fauna. Webby (2004a). The poorly-known caryocaridids were, briefly, among the advance elements of Metazoa invading the pelagic realm above the outer shelf and slope of most continents. But, they are not known from either of the Chinese terranes. Vannier et al. (2003). ATW080301.

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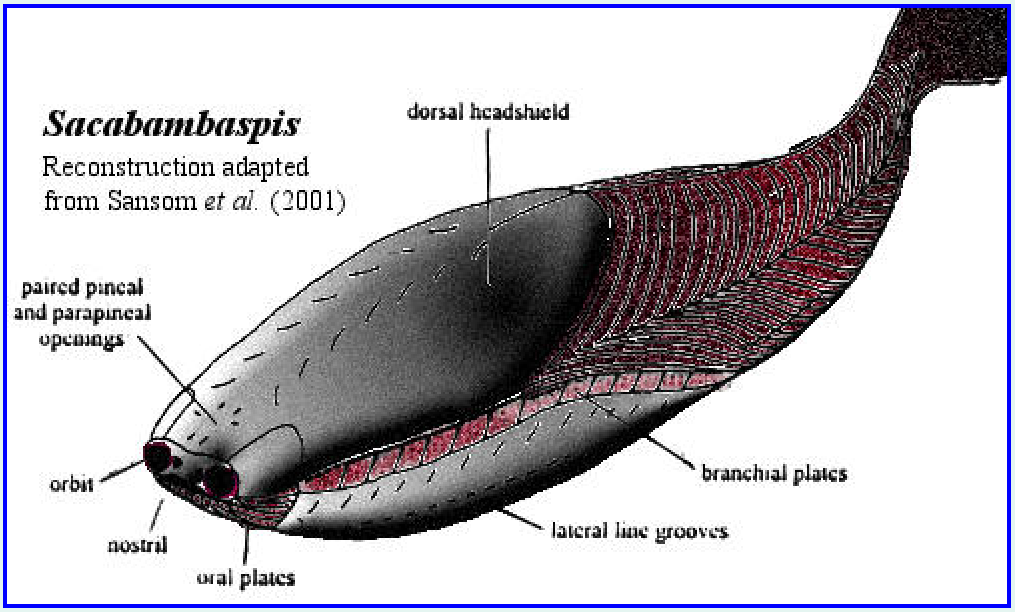
Dapingian - 2

Chordates



Those Ordovician stratigraphic icons, the graptolites, made themselves conspicuous in the Dapingian *Isograptus-Azygograptus* radiation, some members of which are found on every continent. *See*, Stratigraphy. Wang *et al*. (2005). "The first recognizable crinoids with typically constructed cups and columnal-bearing stems, such as *Dendrocrinus*" also appear at about this time. Benton & Harper (1997). Conodonts began a second Ordovician radiation which would last well into the Darriwilian.

The first indisputable fossils of armored jawless fishes are found in the Dapingian or latest Floian. These are the arandaspids of Bolivia and the Amadeus Basin of Australia. These are described by Sansom *et al*. (2001) in the following terms: "The head shields of *Arandaspis* and *Sacabambaspis* are formed from large, roughly oval, dorsal and ventral plates. These headshields are ornamented with characteristic oak-leaf shaped or tear-drop shaped tubercles. The eyes, which are surrounded by what is thought to be endoskeletal bone, and putative nostrils, are found at the extreme anterior of the head, one of the diagnostic features of the arandaspids. Arandaspids are also unique among vertebrates in possessing paired parapineal and pineal openings." ATW080301.

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The Darriwilian (Late Arenig & Llanvirn)

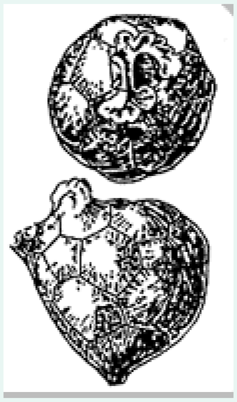
The Darriwilian Age of the Middle Ordovician Epoch: 468 to 461 million years ago

Marine Invertebrates

Trilobites

Ogyginus corndensis
Llandilo, Wales
Found in the Llandeilo flags in great profusion
collected by Tom Levinson
Length: 10 cm

Echinoderms



Canadocystis emmonsi

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modified ATW080302
checked ATW050511
(original page uploaded on Kheper site 15 October 1998)

The Late Ordovician: 1

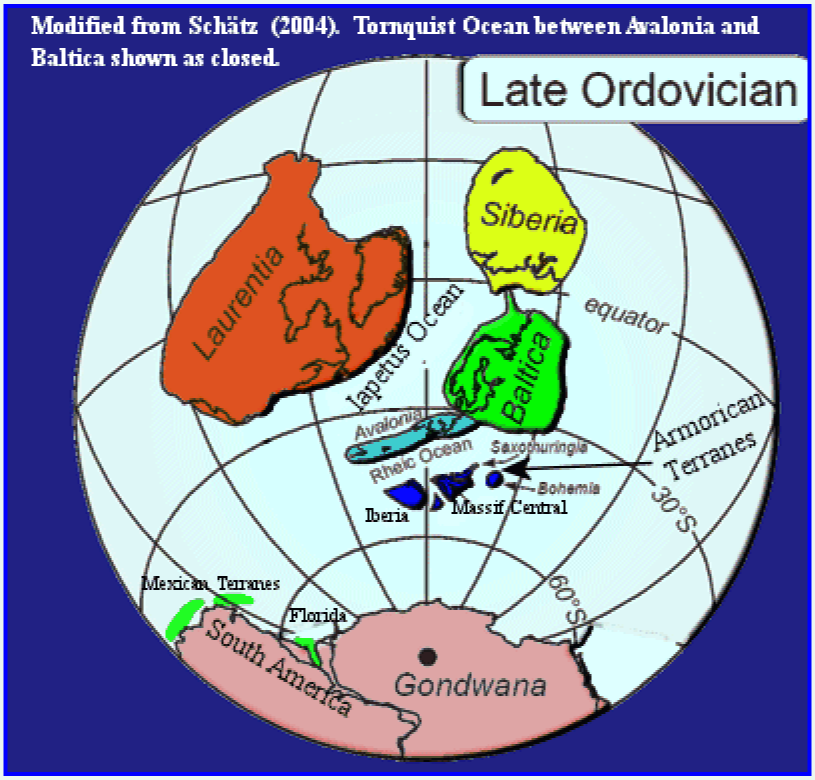
The Late Ordovician Epoch of the Ordovician Period: 461 to 444 million years ago

Introduction

As we have mentioned, the **ICS** has an unreasonable prejudice against **savage Celts**. The Ordovician ages historically bore the proud names of ferocious Welsh tribes. But sadly, under the ICS system, the base of the Late Ordovician is the "Sandbian," with its global type section at (God help us!) F�gels�ng, which means "bird song" or something equally insipid. To make matters worse, the letter '�' -- so far as we are aware -- exists only in Swedish. The Swedes are inordinately proud of the fact that none but a Swede can make this particular noise. We are forced to take this on faith, since all 18 possible vowels in Swedish sound exactly the same to most listeners. We have even toyed with the idea that the supposed differences are audible only at hypersonic frequencies, and that all Swedes in fact possess a unique form of echolocation. Fortunately, however, this page is about the Late Ordovician. Thus it will not be necessary for us to entertain this disturbing conjecture at any greater length.

Geography

The Caledonian Orogeny



Modified from Schätz (2004). Tornquist Ocean between Avalonia and Baltica shown as closed.

We might imagine Ordovician paleogeography as some vast Las Vegas stage, with appreciative crowds (represented by Baltica and Laurentia) applauding chorus lines of smiling, bespangled terranes as they break off from the background of the north Gondwanan margin, kicking and twirling their way across the southern ocean to the steps of some complex, but orderly, tectonic choreography.

Then again, we might not wish to imagine anything of the sort, since we would then be forced to visualize the first few rows of the audience being violently subducted under the inexorably advancing chorus line, the roar of the crowd being swallowed in the volcanic explosions of the Caledonian Orogeny, followed by the howling gale of an Ice Age and mass extinction. This would be ambitious, even for Las Vegas -- more ***G�tterd�mmerung*** than glitz.

The grand collision at the end of the Ordovician occurred in several parts. First was the meeting of Baltica and Avalonia, a chain of terranes which had rifted off the Gondwanan coast early in the Ordovician. The line of islands moved generally northwest, leaving the expanding Rheic Ocean behind it and closing the Iapetus Ocean as it neared the Laurentian margin.

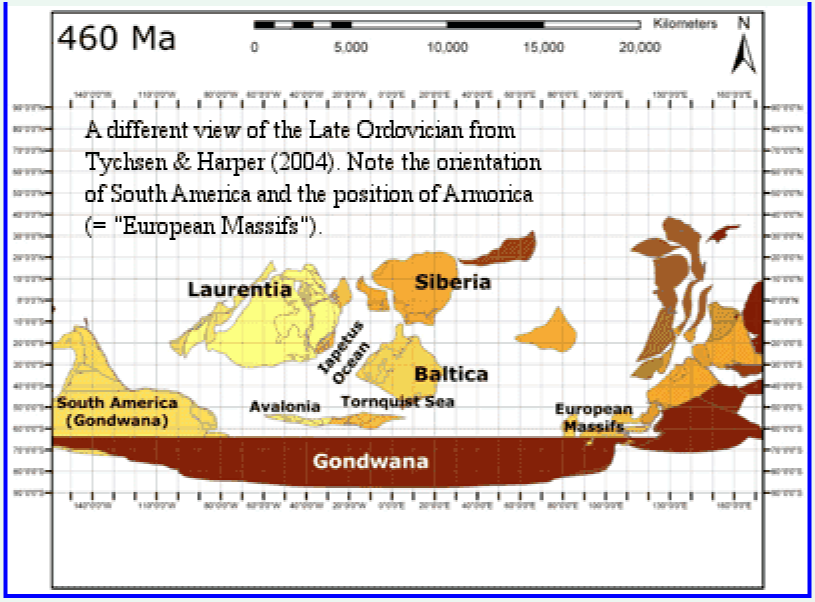
By this epoch, Baltica had slowed its own drive to the north, although it was still gradually crossing the equator. Nawrocki & Poprawa (2006). As Avalonia began to close the Iapetus, its northeastern end also met the western edge of Baltica, closing the Tornquist Ocean. This initiated the Caledonian Orogeny in the north of England. Cocks & Torsvik (2005).

Second, the northern arm of the Iapetus, between Baltica and Laurentia, closed at the endof the Late Ordovician. This triggered an extension of the Acadaian Orogeny into both Baltica and (to a certain extent) Laurentia. The northern portions of Poland, Denmark, and Germany began to form at this time. Nawrocki & Poprawa (2006).

The Avalonian collision was the second of (about) three such events to affect Laurentia and Baltica over the course of the Middle Paleozoic. Stanley (1998). The collision between western Avalonia and Laurentia, and the addition of more Gondwanan blocks, would prolong the Caledonian events into the Early Devonian.

Some of these non-Avalonian fragments, which comprise a significant part of today's Europe, also began to rift from the coast of Gondwana (particularly Africa) during the Late Ordovician. The sequence and timing of these events is less clear than it once was. The original story was that Avalonia was succeeded by Armorica, a second island arc that left Gondwana and more or less followed Avalonia's path across the waves to Baltica and Laurentia. Armorica was said to include parts of Spain, the Massif Central and Brittany of France, the Saxo-Thuringian Plate of Germany, Bohemia (Perunica), Bosnia, and other indispensible components of the European Union. But,in the last few years, geologists have begun to chip pieces off Armorica (Nys�ther et al., 2002; Torsvik & Cocks, 2004), or split it into two separate arcs (Nys�ther et al., 2002). In fact, the tendency now is to discard the whole idea of Armorica as unit and refer to it vaguely as the "Armorican Terrane Assemblage" (Cocks & Torsvik, 2005).

Somewhere to the south of Laurentia was the



South American coast of Gondwana. The intervening ocean may have been narrow. Some geologists (e.g. Ian Dalziel) have argued for actual contact between Laurentia and South America in the earlier Ordovician. However, by the Late Ordovician, several pieces of Mexico and Florida probably covered the northern coast of South America (Ortega-Obreg�n et al., 2008), which was formed by Peru during this epoch.

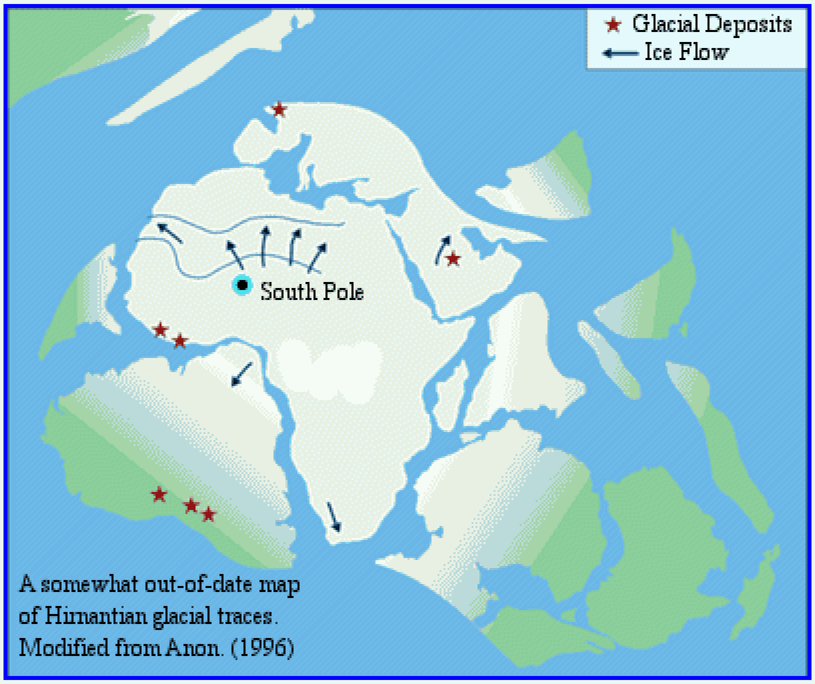
We will defer further discussion of West Gondwana (South America and Africa) until we can take on the Hirnantian Ice Age in general. In fact, we will slide over the rest of the world very quickly, as we've already spent too much of our own, personal time and space on the events in the Laurussian theater.

As in earlier parts of the Ordovician, West Gondwana sat over the South Pole, with the Pole itself wandering nomadically in what is now the Sahara. The rest of Gondwana extended like a sort of gigantic tail northwards from the West Gondwanan head, terminating in the North China craton, which reached north of the equator. This tail remained more or less on the opposite side of the earth from Baltica and Laurentia. North and west of the East Gondwanan tail, some of the Asian blocks were forming. In particular, Siberia was beginning to pick up and consolidate a number of unaffiliated blocks, as discussed in a recent review by Cocks & Torsvik (2007). ATW080321.

Climate

The End-Ordovician Ice Age

For the most part, the Late Ordovician climate was like the Middle Ordovician climate, but more so. The world continued warm, with two episodes of global warming in the early and middle or late Hirnantian. Cocks & Torsvik (2005). The seas continued to rise. Stanley (1998). All this, as we will see, was good for life. But it ended, quite suddenly (Webby, 2004) with a brief ice age at the end of the Hirnantian.



A somewhat out-of-date map of Hirnantian glacial traces. Modified from Anon. (1996)

This particular ice age seems to have been quite different from those of the Proterozoic or Pleistocene. It was perhaps similar to the ice age(s) of the Mississippian, but considerably shorter. On the evidence of oxygen isotope excursions, the end-Ordovician event lasted only about 500,000 years. Stanley (1998). Even so, it seems to have included several distinct periods of glaciation. It is unclear exactly how many glacial events there were. Depending on location, there may have been only one, or as many as five.

These are minimum figures, based on the number of successive layers of glacial till. It is entirely possible that, in any given location, a late glacial event might destroy all evidence of earlier events. Yet there's bit of a pattern. Ghienne *et al*. (2007) find two cycles in Algeria. Le Heron *et al*. (2006) located four in Libya. Connally & Wiltse (1996) describe five in Saudi Arabia. This suggests that the south polar region retained a permanent ice cap, which expanded east or contracted west, depending on the severity of the various glacials and interglacials. Unfortunately, we must also entertain the possibility that the events may, instead, have been localized and asynchronous, since one of the Saudi events has been ascribed to the Rhuddanian (earliest Llandovery).

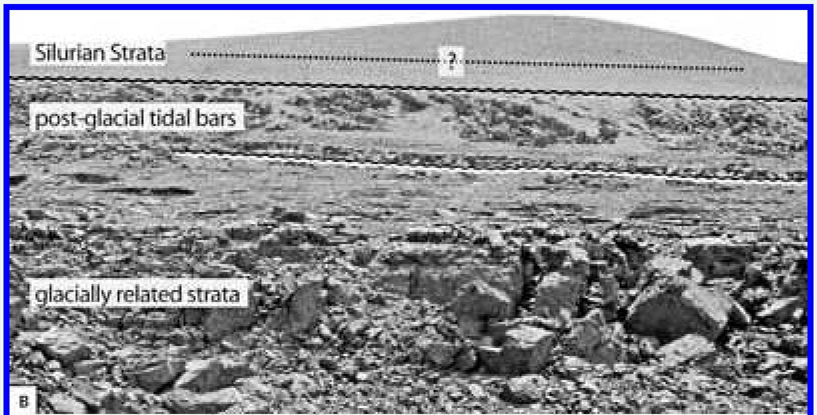
Low-angle swaley cross-stratification, diagnostic of ice-free shelf with storm-driven flows, just north of the North African Basin. From Le Heron *et al.* (2006).

Perhaps more interesting is the nature and movement of the ice sheets. In the map from Connally and Wiltse, note how the main flow is directed into a North African basin, not off the nearest edge of the continental platform. This is confirmed by the studies cited above. In addition the ice flow was highly heterogeneous. That is, it included numerous ice rivers which moved quite quickly while adjacent ice remained almost stationary. The bases of the ice sheets show considerable evidence of subglacial melting and substantial flows of meltwater undercutting the ice.

Two other data are interesting. First, Le Heron *et al*. (2006) emphasize the local importance of a glacial trampoline effect: subsidence caused by the weight of the ice sheet, followed by post-glacial rebound. This is peculiar for a short-lived ice sheet which ought not to have been particularly thick. Second, Ghienne *et al*. (2007) argue that, contrary to conventional wisdom (e.g. Benton & Harper, 1997; Stanley, 1998), the Hirnantian ice age occurred during a time of rising sea levels. They assert that the maximum intrusion of marine conditions into the interior of Africa (as judged by the presence of graptolites and other marine forms) did not occur until the earliest Silurian.

As you have probably guessed, we have not presented these particular facts merely for the general edification of the reader, but rather to introduce yet another futile and unsubstantiated speculation on a subject we are grossly unqualified to address: to wit, the cause of the Hirnantian ice age. But that is the trade-off at the heart of Palaeos. The reader obtains the questionable benefit of our research into the facts, while we are permitted to imagine that someone may imbibe the facile concoctions we brew to make sense of the data.

Our thought is that the Hirnantian ice required only a deep south polar basin and a rising sea. Without question, the oceans gradually transgressed over northern Africa over the course of the Ordovician. At some point, the seas filled the North African Basin. However, contact with the ocean was initially limited and irregular. It may well have been limited to occasional storms, since tempestites and other indicators suggest that the area to the north of the basin was (during the earliest phase of glaciation) "an open shelf that was free of sea ice ... and that was subject to episodic, very high-energy storms." Le Heron *et al*. (2006).



Upper portion of the Hirnantian glacial sequence in Libya. Ghienne *et al.* (2007)

Since contact with open water was limited, the basin filled with a large volume which was thermally isolated from the oceans and located at or near the South Pole. Consequently, it froze. When it had frozen through, the weight of the ice locally depressed the basin further, accommodating more water. At this point, the coldest regions episodically become cold enough to accumulate "real" ice sheets through precipitation. Given the geography of the area, we would expect to see this ice forming near the Pole and flowing generally eastward (paleo-northeast) from Algeria into Libya and Arabia. This should occur, both because the coldest regions would lie westward and because the west end was in closest contact with the ocean. The west (Algeria) would thus be permanently frozen, while locations to the east would show an increasing number of episodic glacial "events."

At the same time, the ocean would continue to contribute water, which would melt and undermine the basin ice, perhaps causing the complex pattern of ice flow and subglacial melting actually observed. Over the slightly longer run, the rising seas outpaced the growth of the ice sheet and established regular contact with the north African basin.

This ended the thermal isolation of the South Polar region. At this point, the ice cap would melt quickly. Isostatic rebound of the crust would briefly displace water, which, together with generally rising sea levels, briefly flooded additional areas post-glaciation, as observed by Ghienne *et al*. (2007). But the era of rising seas was now over, and the ocean began to retreat from the Sahara early in the Silurian. ATW080322.

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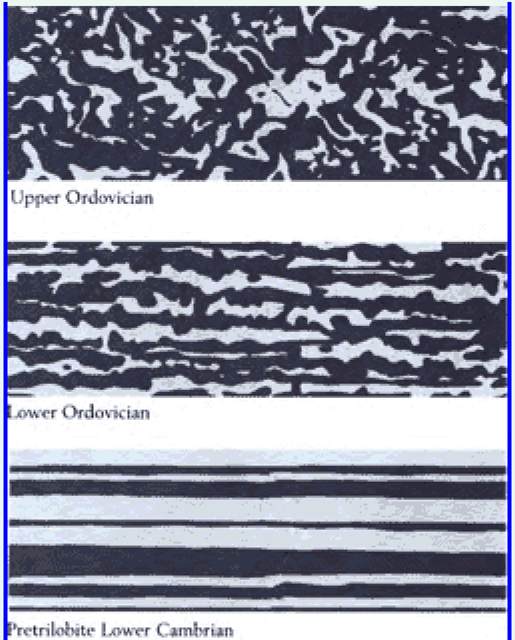
The Late Ordovician: 2

Life

The GOBE

The Late Ordovician was the high point of the mass anti-extinction called the Great Ordovician Biodiversity Event (*GOBE*). With rare exceptions (graptolites, rostroconchs), all animal groups present in the Late Ordovician attained their highest diversity in that epoch (Webby, 2004a) and global genus-level animal diversity came close to its Paleozoic maximum (Stanley, 1998).

There are any number of plausible reasons why this occurred. Warm epicontinental seas have always promoted the expansion of animal life, and these conditions prevailed in Laurentia, Baltica, Avalonia, Australia, China, Siberia, Mongolia and Kazakh. At the same time, the cool to cold waters circulating across the long coast of West Gondwana encouraged the evolution of different forms adapted to those conditions. The continents were widely scattered, providing both a larger area of coastal and shelf environments and a large number of partially isolated ecosystems in which species would necessarily diverge through genetic drift.



Early Paleozoic styles of bioturbation. Stanley (1998)

In addition, the diversity of benthic environments increased. The shift to "calcite" seas meant an increase in the area of carbonate shelf, and the Late Ordovician has thus been described as the "Golden Age of hardground epizoonts." Taylor & Wilson (2003). At the same time, the intensity and depth of softground bioturbation was increasing, greatly expanding the volume of mud & crud environments for mud-sucking worms (or "softground benthic infauna," if you must) and their predators. Stanley (1998). ATW080322

Dissecting the GOBE

For the general run of animal life, the GOBE consisted of two diversity peaks separated by a slight dip, followed by a crash in the Hirnantian ice age. The peaks occurred in the "mid Caradoc," which we translate as Late Sandbian, and the "mid Ashgill," which we suppose to be the mid to late Katian. Webby (2004a). Webby asserts that the Sandbian peak was both lower and more gradual than the abrupt rise in the Katian Age. That is, the Sandbian peak was merely a continuation of the Darriwilian trend line. The slight dip between the peaks may be associated with an event of uncertain nature which resulted in the loss of various groups of Laurentian brachiopods and ostracodes in northern Baltica. *Id*.

Krug & Patzkowsky (2004) raise some serious questions about the methodology supporting this type of analysis. They attempt to correct for sampling bias and find, when this is done, that most of the temporal fine detail disappears. Animal diversity beaks broadly into the first half of the Katian and then remains relatively constant, declining slightly through the rest of the Katian before crashing in the Hirnantian. Yet Cocks & Torsvik (2005) make the qualitative, but weighty, point that the later Katian was marked by an episode of warming "which led to the formation of substantial carbonate mud mounds (bioherms) with very diverse brachiopods, trilobites, molluscs, echinoderms and bryozoa." Ultimately, we do not yet know enough about the fossil record, and the statistical techniques needed to analyze it. The GOBE certainly happened, but its precise contours are still hazy. ATW080322.

The Freeze

We have covered the timing and mechanics of the Hirnantian ice age above. The effects of this cold snap on life were variable. Plainly, many species became extinct -- 70% of all animal species, according to one estimate. Benton & Harper (1997). Many common families of Ordovician brachiopods, echinoderms, ostracodes, and trilobites disappeared entirely. Many others shifted their ranges. *Id.* The end of the cooling caused yet further evolutionary angst (Stanley, 1998; Krug & Patzkowsky, 2004), as groups which had just worked out how to adapt to colder conditions became frustrated with an environment that capriciously changed its mind and wanted everything back the way it had been before it installed a state-of-the-art South Polar ice cap. We admit that we have seriously considered extinction ourselves, under similar circumstances.

A 70% *species*-level extinction wouldn't involve much family level extinction at all, if the extinct species were randomly distributed. Further, to use an industrial analogy, this extinction did not represent the kind of wholesale elimination of jobs groups which occurs when the local factory closes, or when technology replaces assembly lines with assembly language. The end-Ordovician is more closely analogous with the case in which two local firms merge and become a regional producer. Some jobs become redundant, some become more specialized, and some new ones are created. Many individual lives and careers are drastically altered, for better or worse, but the overall economic dislocation is minor and temporary.

In one sense, this analogy is exact. The physical merger of Avalonia, Baltica, and Laurentia wouldn't leave room for three different species of brachiopod that did exactly the same thing. These species would specialize or become extinct. To that extent, an end-Ordovician extinction would have occurred with or without an ice-age. Similarly, any rapid series of environmental changes will favor generalists over specialists. By definition, generalists will overlap in ecospace more than specialists, and diversity will necessarily suffer. As human beings, we are in a particularly poor position to complain about that result. Finally, the ice-age almost completed the Ordovician trend toward replacing the old Cambrian fauna, *e.g*. trilobites and "inarticulate" brachiopods, with the characteristic animals of the Paleozoic, *e.g*. stromatoporoids, corals, conodonts, and brachiopods which, if no more eloquent than their ancestors, were none the less articulate enough for the needs of the Silurian. ATW080323.

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Sandbian (Early-Middle Caradoc)

The Sandbian Age of the Late Ordovician Epoch: 461 to 456 million years ago

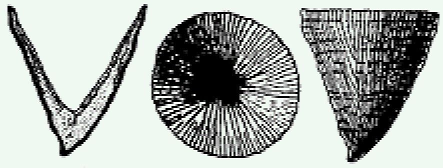
The Ordovician has been quite significantly revised in recent years. The traditional division of the Late Ordovician into the Caradoc and Ashgill has been replaced by a three-part division. The first of these is the Sandbian, which is more or less equivalent to the Early Caradoc and most of the Middle Caradoc. The Katian includes the Late Caradoc and all of the Ashgill prior to the start of serious global cooling. The Hirnantian, formerly a stage of the Ashgill, is now the final age of the Ordovician. ATW080323.

Marine Invertebrates

Phylum Cnidaria

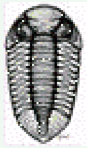
Class Anthozoa

Rugose Corals



Lambeophyllum profundum (Conrad)
specimen about 2.5 cm long and in diameter
Blackriveran age (Harnagian)
New York
(reference: Moore, Lalicker & Fischer, *Invertebrate Fossils*, p.114)

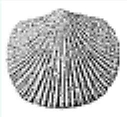
Trilobites



Calyptaulax callicephalus
dalmanitid trilobite - family Pterygometopidae
Black River and Trenton Groups
(= Harnagian to Longvillina)
eastern and northeast Canada, and New York state

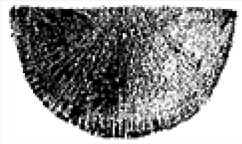
Phylum Brachiopoda

Order Orthida
Family Dalmanellidae



Paucicrura rogata (Sardeson)
shell about 7mm long and wide
Trenton Group
North America
more on Paucicrura
(at the Union College Geology Department site)

Order Strophomenida
Family Sowerbyellidae



Sowerbyella sericea (Sowerby)
Sandbian
England
shell about 1 cm wide
more on Swerbyella
(at the Union College Geology Department site)

Links

Mohawk Valley Fossils - a very informative site, put together by the Union College Geology Department. Detailed surveys of occurrences of fossils of creatures that lived during Late Sandbian to Early Katian times (probably Longvillian and Actonian).

Ordovician Trentonian fauna from the Galena and Maquoketa of West DePere and Green Bay Wisconsin

The Katian

The Katian Age of the Late Ordovician: 455.8 to 445.6 million years ago

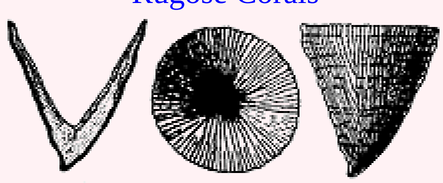
The Ordovician has been quite significantly revised in recent years. The traditional division of the Late Ordovician into the Caradoc and Ashgill has been replaced by a three-part division. The first two ages of the Late Ordovician were recently (2005) named the Sandbian and Katian Ages. The Sandbian is equivalent to the Early Caradoc. The Katian is equivalent to the Late Caradoc and Early Ashgill. The Hirnantian, formerly a stage of the Ashgill, is now the final age of the Ordovician. The base of the Katian is defined as the first occurence of the graptolite *Diplacanthograptus caudatus*, just below the base of the Guttenberg carbon-13 isotope excursion. The GSSP is located 4 m above the base of the Bigfort Chert, Black Knob Ridge section, 5 km northeast of Atoka, Oklahoma, USA.

Marine Invertebrates

Phylum Cnidaria

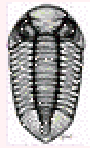
Class Anthozoa

Rugose Corals



Lambeophyllum profundum (Conrad)
specimen about 2.5 cm long and in diameter
Blackriveran age (Harnagian)
New York
(reference: Moore, Lalicker & Fischer, *Invertebrate Fossils*, p.114)

Trilobites



Calyptaulax callicephalus
dalmanitid trilobite - family Pterygometopidae
Black River and Trenton Groups
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eastern and northeast Canada, and New York state

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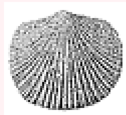
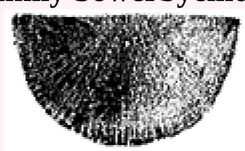
Family Dalmanellidae



Paucicrura rogata (Sardeson)
shell about 7mm long and wide
Trenton Group
North America
more on Paucicrura
(at the Union College Geology Department site)

Order Strophomenida
Family Sowerbyellidae



Sowerbyella sericea (Sowerby)
Caradoc
England
shell about 1 cm wide
more on Swerbyella
(at the Union College Geology Department site)

Links

Links

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Ordovician Trentonian fauna from the Galena and Maquoketa of West DePere and Green Bay Wisconsin

TAXA REPORTED FROM THE TYPE-CINCINNATIAN ALPHABETICAL LISTING BY GENUS (late Caradoc Actonian onwards) to late Hirnantian

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The Katian (Late Caradoc-Middle Ashgill)

The Katian Age of the Late Ordovician Epoch: 456 to 446 million years ago

Introduction

The Ordovician has been quite significantly revised in recent years. The traditional division of the Late Ordovician into the Caradoc and Ashgill has been replaced by a three-part division. The first two ages of the Late Ordovician are the Sandbian and Katian Ages. The Sandbian is equivalent to the Early Caradoc. The Katian is equivalent to the Late Caradoc and Early-Middle Ashgill. The Hirnantian, formerly the last stage of the Ashgill, is now the final age of the Ordovician. The base of the Katian is defined by reference to the first occurrence of the graptolite *Diplacanthograptus caudatus*, just below the base of the Guttenberg carbon-13 isotope excursion. The GSSP is located 4 m above the base of the Bigfort Chert, Black Knob Ridge section, 5 km northeast of Atoka, Oklahoma, USA.

Stratigraphy

When the ICS first set out to map the Ordovician in 1960, the task may have looked routine. The Ordovician System was about as old as stratigraphy itself, and the British system was used by nearly everyone, nearly everywhere in the world. As it turned out, this unanimity of historical practice masked conflicts in the data which could not be resolved. The foundation of the British Late Ordovician rested on a peculiarly British fauna which didn't play well with global graptolite zones. Consequently, almost everything had to be reworked. Chen *et al*. (2006). This is a good thing for us, because it has generated a great many high-quality stratigraphic studies within the last decade or so. Even so, local correlations have not been able to keep up with the changing names and biostratigraphy. Our usual desultory review of the literature has allowed us to construct only the following, and with many uncertainties at that:

Global Timeslice Webby (2004)	**North American Graptolite Zone** Nardin (2007); Stott & Jin (2007)	**ICS Stage**	**North America** Stott & Jin (2007)	**Britain** Stott & Jin (2007)	**Bohemia** Nardin (2007), Ausich et al. (2002).	**Baltic** Paškevicius (2007)	**Siberia** Cocks & Torsvik (2007)
6c	*Normalograptus extraordinarius*	**Hirnantian**		(Hirnantian)	Kosovian	Porkuni	Burian?
6b	*Parorthograptus pacificus*		(Gamachian)	(Rawtheyian)		Pirgu	Ketski
6a	*Dicellograptus complanatus & Diplograptus ornatus*			(Cautleyian)		Vormsi?	Nirundian
5d latest			(Richmondian)??		Králodvorian (Avalonian Ashgill)		
5d late				**Ashgill** (Pusgillian)		Nabala?	
5d mid	*Amplexograptus manitouliensis*		(Maysvillian)				Dolbor?
5d early?	*Geniculograptus pygmaeus*		**Cincinnatian** (Edenian)	(Steffordian)		Rakvere?	
5c	*Diplacanthograptus caudatus*	**Katian**	(Trentonian?)	(Cheneyian-Steffordian)		Oandu	Baksan?
5b	*Climacograptus bicornis*	**Sandbian**	**Mowhawkian** (Black River?)	Caradoc (Burrellian)	Berounian	Keila	Chertov

Climate

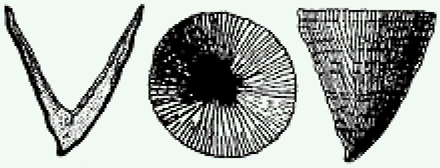
The Katian largely reflected the peak of the overall global warming trend of the Ordovician. However, there are some indications of a brief cold spell towards the middle of the Katian, perhaps coincident with the traditional Caradoc-Ashgill boundary. This is reflected in changes of sedimentation patterns in Baltica (Cocks & Torsvik, 2005) and a minor dip, or at least leveling off, in the global diversity profiles of many animal groups (Webby, 2004a). On the other hand, both may be explained by the merger of Avalonia, Baltica and Laurentia which began at this time. The closing of the northern Iapetus Ocean in the Katian would certainly have affected coastal currents in some fashion, and it clearly resulted in a sorting out of the endemic marine fauna around the three continents. Cocks & Torsvik (2005); Hints *et al*. (2007). The exact locations of Siberia and Perunica at this time are unclear, but they, too, seem to have been close enough to Baltica for some degree of faunal exchange to take place. Cocks & Torsvik (2002); Tychsen & Harper (2004); Cocks & Torsvik (2007).

What all this does *not* explain is the interesting pattern of radiolarian evolution. Radiolarian diversity peaked around the mid-Katian. The group seems to have begun its decline well-before the Hirnantian (Webby, 2004a), and this may suggest a generally less healthy open marine environment. A similar pattern is found in other environmentally-sensitive groups, such as sponges (Webby, 2004) and some brachiopods. *Id.*

Invertebrates

Cnidaria

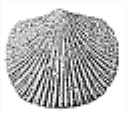
Rugose Corals



Lambeophyllum profundum (Conrad)
specimen about 2.5 cm long and in diameter
Blackriveran age (Harnagian)
New York
(reference: Moore, Lalicker & Fischer, *Invertebrate Fossils*, p.114)

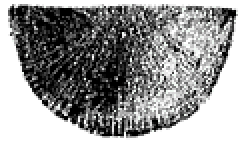
Brachiopoda

Order Orthida
Family Dalmanellidae



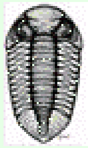
Paucicrura rogata (Sardeson)
shell about 7mm long and wide
Trenton Group
North America
more on Paucicrura
(at the Union College Geology Department site)

Order Strophomenida
Family Sowerbyellidae



Sowerbyella sericea (Sowerby)
Caradoc
England
shell about 1 cm wide
more on Swerbyella
(at the Union College Geology Department site)

Arthropoda



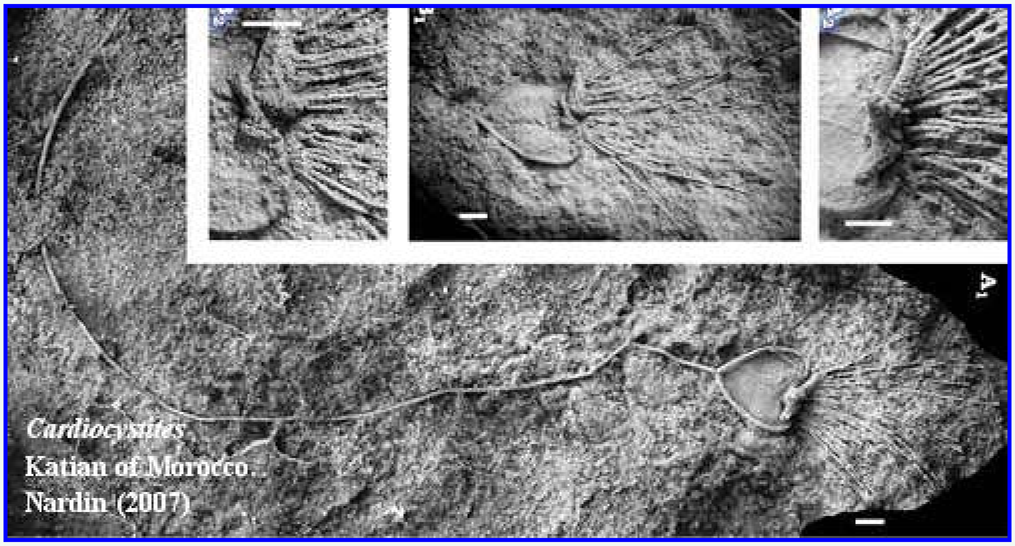
Calyptaulax callicephalus, dalmanitid trilobite - family Pterygometopidae. Black River and Trenton Groups (Sandbian-Katian boundary),

The Megalograptoids are, despite the name, eurypterids. *Megalograptus* is, in fact, the first apparently widespread genus of eurypterid, and its remains have been found in several Katian locations in eastern Laurentia from Quebec to Virginia. It is not certain that they actually evolved in Laurentia. The earliest known eurypterids are from the Sandbian of Wales. However, for most of their history, they remained largely in eastern Laurentia, Avalonia and western Baltica. Tetlie (2007).

Several substantial swimming trilobite groups evolved during the Late eastern and northeast Canada, and New York state.

Ordovician, peaked in the Katian and became extinct shortly thereafter. Webby (2004a). Meanwhile, the characteristic Paleozoic arthropod fauna, including eurypterids, phyllocarids, and ostracodes, continued to expand. *Id*.

Echinodermata



The Katian was an exuberant time for echinoderms. Almost all of the major echinoderm clades had Katian representatives: asteroids, crinoids, diploporans, eocrinoids, edrioasteroids, ophiuroids, rhombiferans, solutes, and stylophorans. Recent work on the eocrinoid *Cardiocystites* suggests that these primitively epibenthic forms evolved adaptations to lift themselves off the bottom, using long (10-20 cm), flexible stems to fix themselves to the bottom, while the theca floated above. This system presumably allowed these echinoderms to feed well above the bottom, even in high-energy environments, without being swept away. In fact, with this tether, a faster current would only increase the flow of food items available to the animal. The strategy seems to have been a success, as specimens of *Cardiocystites* are known from Britain, Gondwana (Morocco) and Perunica (Bohemia). Nardin (2007). This globalization is typical of Late Ordovician echinoderm groups. Ausich et al. (2002).

Vertebrates

As discussed in at various other points, a relatively complete set of primitive vertebrates had also appeared by the Katian. Any Ordovician vertebrate remains are still rare, but thelodonts, in particular, become considerably more common in the Katian -- specifically in Timan-Pechora and other terranes of present-day Asia. The Katian (or perhaps Sandbian) also produced the last major group of early Paleozoic vertebrates, the Acanthodii, a group of fish close to our own ancestry. Sansom *et al*. (2001). Since acanthodians and sharks are both known by the Katian, we can be relatively certain that jaws had evolved by this time. This useful addition to the vertebrate repertoire seems to have taken a little while to perfect, since the great radiation of gnathostome fishes was still more then 20 My in the future.

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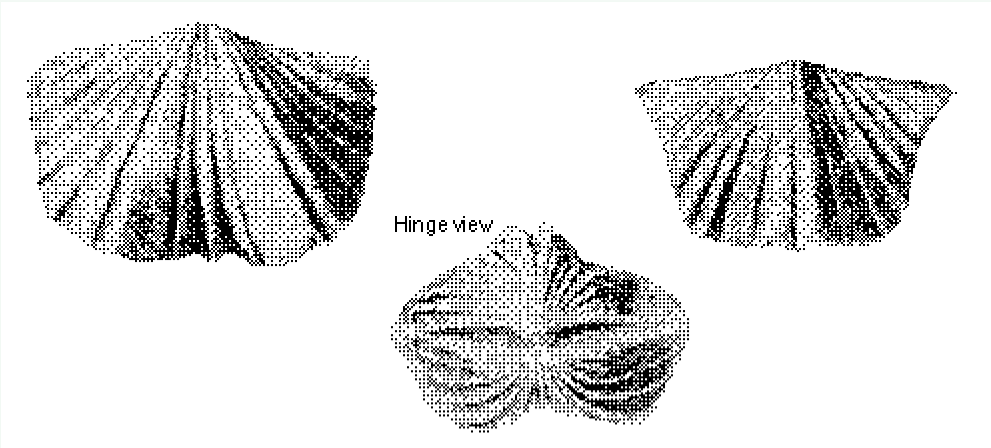
The Hirnantian

The Hirnantian Age of the Late Ordovician Epoch: 446 to 444 million years ago

Introduction

The Ordovician has been quite significantly revised in recent years. The traditional division of the Late Ordovician into the Caradoc and Ashgill has been replaced by a three-part division. The first two ages of the Late Ordovician are unnamed, and are referred to as Ordovician V and VI. Sandbian is equivalent to the Early and Middle Caradoc. Ordovician VI is equivalent to the Late Caradoc and Early Ashgill. The Hirnantian, formerly a stage of the Ashgill, is now the final age of the Ordovician. ATW040316

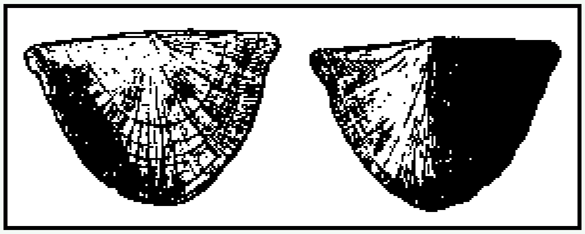
Marine Invertebrates



Phylum Brachiopoda
Order Orthida
Family Plectorthidae

Platystrophia laticosta *Meek*

Horizon: Maysville Group (early Hirnantian epoch - Pusgillian Age)
Locality: southern USA
Size: shell about 2 to 2.5 cm wide
Links: More on *Platystrophia* (at the Union College Geology Department site)



Phylum Brachiopoda
Order Strophomenida
Family Strophomenidae

Rafinesquina loxorhytis *(Meek)*

Horizon: Richmondian
Locality: Indiana
Weight:
Size: shell about 7 cm wide
Links: more on *Rafinesquina* (at the Union College Geology Department site)

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Notes & References

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Notes

[1] The "top five" are, more or less in order, the end-Permian, the Ordovician Ice Age, the KT, the Frasnian-Famennian events, and the end-Jurassic. In our opinion, the last two scarcely count. TheFrasnian-Famennian extinctions actually began in the Middle Devonian and were too diffuse to be treated as a single event. The end-Jurassic was a case of accelerated turnover, with scarcely any decrease in overall diversity.

[2] Hence the name of the Floian. To be fair, the name could have been worse. The main competitor of Flo for the stratotype section was "The Ledge" on the Cow Head Peninsula of Newfoundland.

[3] The graptolites did not become extinct at that time -- or perhaps ever. We haven't done our homework on this one, but there is respectable opinion that the graptolites include the living pterobranch worms. See, for example, the citations at **graptolite.net**. Certainly, the graptolites lasted into the Mississippian.

[4] "... notre pays, r�put� ingouvernable, capricieux, schizophr�ne ..." Yves Thr�ard, *Le Figaro* (Paris) 22/02/08. Bien s�r, avec raison, et depuis longtemps...

[5] *B. triangularis* had also been considered and rejected in favor of *T. laevis* during the 1995 selection of the Middle Ordovician guide event. Wang *et al*. (2005).

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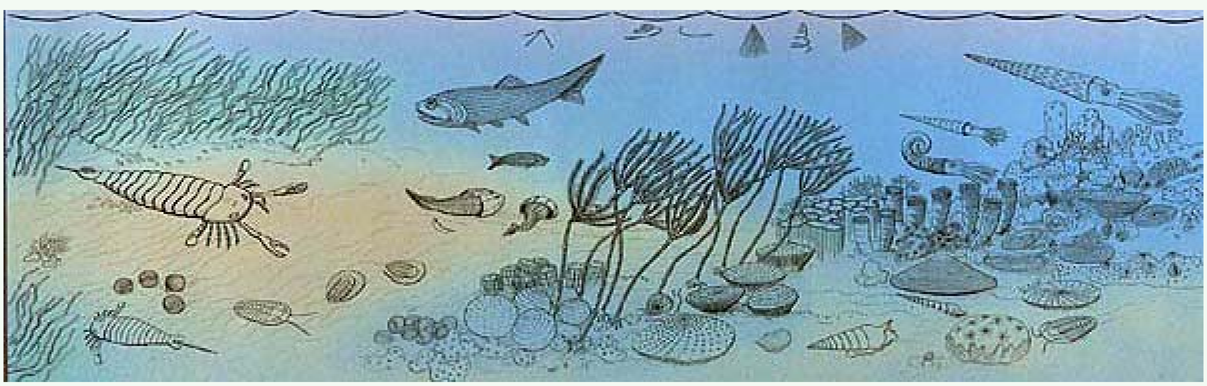
Silurian period

Palaeos com is currently undergoing a major revision and update. For this reason, you may find many blank pages, broken links, etc. We hope to have some material on this page soon. Thank you for your patience.

Silurian Period

The Silurian

The Silurian Period of the Paleozoic Era: 444 to 416 Mya



graphic © from Naturmuseum Senckenberg (Centre for Biodiversity Research)

drawing shows Eurypterids, rhynchonelid brachiopods, and trilobites (***left***); primitive fish, more brachs, various types of corals, stalked crinoids, archaeogastropod, and drifting graptolites (***center***); and more corals, another trilobite, and several types of nautilod cephalopod (***right***)

History

During the 1830s the great English geologist Sir Roderick Impey Murchison was studying fossiliferous strata outcropping in the hills of South Wales. He named this geological stage the Silurian System, after the *Silures*, an ancient Celtic tribe that lived along what is now the Welsh-English border. In 1835 Murchison and Sedgwick presented a joint paper, *On the Silurian and Cambrian Systems, Exhibiting the Order in which the Older Sedimentary*

Strata Succeed each other in England and Wales, which laid the foundation for the modern geological time scale. During the following years a bitter controversy arose between the two former friends over the relative status of the Cambrian and the Silurian. This was only resolved in 1879 by the formulation of a further, Ordovician period as intermediate between the two stages.

Geography

The early Paleozoic saw the continents clustered around the equator, with Gondwanaland continues it's slow southern drift. Meanwhile Siberia, Laurentia and Baltica converge at the equator. By the end of the Silurian, these colliding continents had began to raise mountains and forge a new supercontinent, Laurussia.

Stratigraphy

Period/System	Epoch/Series	Age/Stage	When began
Devonian	**Early Devonian**	**Lochkovian**	**416.0 mya**
Silurian	**Pridoli**	**(not subdivided)**	**418.7**
	Ludlow	**Ludfordian**	**421.3**
		Gorstian	**422.9**
	Wenlock	**Homerian**	**426.2**
		Sheinwoodian	**428.2**
	Llandovery	**Telychian**	**436.0**
		Aeronian	**439.0**
		Rhuddanian	**443.7**
Ordovician	**Late Ordovician**	**Hirnantian**	**445.6**

See also the very useful biostratigraphic chart at **Silurian Time Scale**.

Climate

The Earth entered a long warm greenhouse phase. However latitudinal variations in climate were rather similar to today, with glaciers occurring in the higher latitudes (over 65^{o}). Regions of marked aridity occurred within 40^{o} of the Silurian equator. Warm shallow seas covered much of the equatorial land masses.

Silurian Sites

The Much Wenlock Limestone Formation

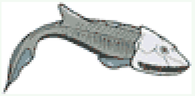
The Much Wenlock Limestone Formation of Britain reveals one of the most diverse, and well-preserved fossil assemblages known, with well over 600 species of invertebrates recorded. The Much Wenlock Limestone Formation of Wales and the Welsh Borderland contains a diverse fauna of well over 600 species (mainly crinoids, corals, brachiopods, trilobites, algae and bryozoans) deposited during the early Silurian when this area was covered by a relatively warm, shallow shelf sea. The Crinoidea account for around 10% of this number with an estimated 35 genera and 56 species.

> "The Much Wenlock Limestone Formation of Wales and the Welsh Borderland contains a diverse fauna of well over 600 species (mainly crinoids, corals, brachiopods, trilobites, algae and bryozoans) deposited during the early Silurian when this area was covered by a relatively warm, shallow shelf sea. However, the Wenlock bryozoans remain poorly studied and understood, even though they constitute an important part of the fauna. Species concepts are often insufficient, and there is a need for revised descriptions, incorporating thin-section work. Furthermore, phylogenetic, ecological and functional morphological studies also need to be carried out, as these areas have not been investigated in detail. Preliminary work on one particularly characteristic Wenlock bryozoan, *Ptilodictya lanceolata* (Goldfuss, 1829), a cryptostome, has revealed new information on its functional morphology, together with patterns of seasonal development based on zooid measurements. In addition, multivariate statistical analyses are currently being used to review the fenestrate species. Past workers have relied too heavily on the so-called 'micrometric formula' and, as a result, taxonomically important characters have often been overlooked, and little thin-section work has been carried out. It is hoped that this research, utilizing a wider range of characters, will provide a reliable taxonomic platform for the study of Silurian bryozoan phylogeny and palaeoecology" (Snell 1999).

The Crinoids of Much Wenlock

> "The Much Wenlock Limestone Formation of Britain reveals one of the most diverse, and well-preserved fossil assemblages known, with well over 600 species of invertebrates recorded. The Crinoidea account for around 10% of this number with an estimated 35 genera and 56 species. The high quality of preservation has revealed a range of small-scale morphological features among the aboral surfaces of the arms and calyces of this group. Small, circular to sub-circular depressions and parabolic traces are randomly situated in the calcite plates of a number of the crinoid taxa. A small number of these features indicate *in vivo* formation through the presence of rims and gall-like features surrounding the trace. These structures are interpreted as a response by the crinoid to the presence of another organism through either a mechanical or a chemical stimulant. The lack of penetration into the body cavity and the extent of the reaction structures suggest a symbiotic relationship existed between host crinoid and trace maker. A high degree of host-selectivity is observed with only 15% of crinoid species being affected. This number includes some of the most abundant crinoid species in fossil collections as well as a number of much rarer species. Work is now commencing on the taxonomic identity of the pit-producing organisms" (Widdison 1999).

Life - the Biosphere



Following the Ordovician extinction event there was a rapid recovery of invertebrate faunas during the Silurian. The high sea levels and warm shallow continental seas provided a hospitable environment for marine life of all kinds. The biota and ecological dynamics were basically still similar to that of the Ordovician, but was more diverse

Brachiopods are the most common hard-shelled organisms, making up 80% of the total species. Among these, pentamerids first appear and are abundant, rhynchonellids, and the spire-bearing athyridids and atrypidids are also common, as are other groups that continue from the Ordovician.

Tropical reefs are common in the shallow seas of this period, formed by tabulate and rugose corals, stromatoporoid organisms, bryozoa and calcareous algae. Trilobites, cephalopods, gastropods, and echinoderms. The Trilobites, having reached their acme in the Cambrian and Ordovician, are now in decline. The trinucleids and asaphids are absent, whilst encrinites and illaenids do not survive the end of the Silurian

Planktonic graptolites remain common and diverse. The single-spined *Monograptus* is the predominant genus, and its species are useful as zone fossils.

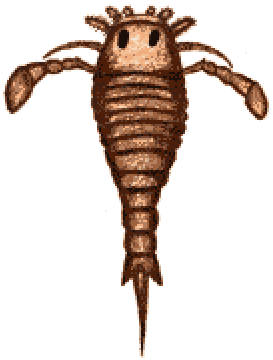
Jawless fish invade brackish and fresh water, as do eurypterids, xiphosurids, scorpions, which may have been semi-aquatic. rhyniophytes, primitive lycophytes, and myriapods became the first proper land organisms. At the end of the period Jawed fish appeared for the first time, but they remain insignificant.

Some Typical Silurian Organisms

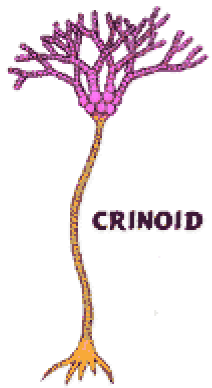
Gastropod

Platyceras

Eurypterid



Echinoderm



Jawless fish

Silurian Ecosystems

Benthic

A Silurian sea floor, showing numerous tabulate corals of the genus *Favosites* large Stromatoporoids, the "sunflower coral" (possibly a green alga) *Ischadites*, and rugose corals of the genera *Entelophyllum*, *Kodonophyllum*, *Streptelasma* and *Craterophyllum*. Crawling among the coral and stromatoporoids are various kinds of gastropods. In the background are crinoids of the genus *Laubeocrinus*, and orthocerid straight shelled nautiloids (*Kionoceras*).

url - image originally from Spinar, **Life Before Man**

Pelagic

Silurian pelagic organisms included planktonic graptolites, trilobites, (although most were crawlers, some were swimmers), crustaceans, "thelodont" jawless fish, and cephalopods

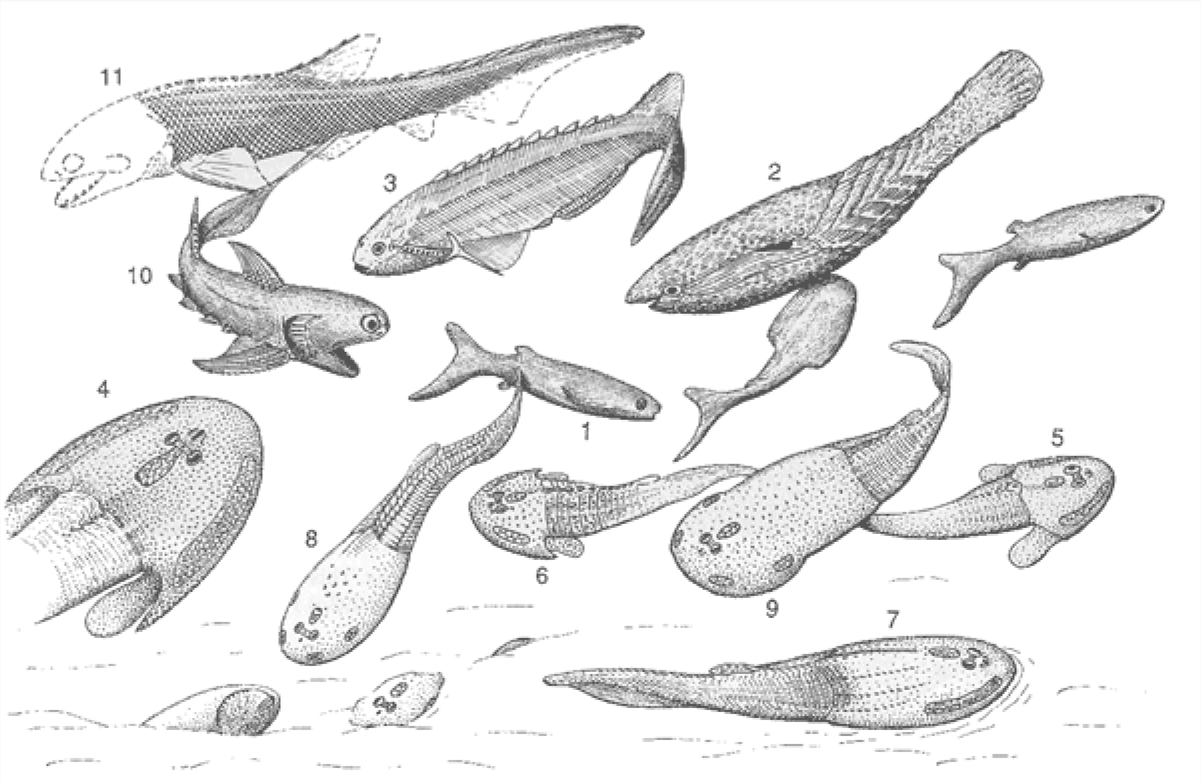
Of all of these, the cephalopods were the largest and most impressive animals of the marine biota. While most were pelagic or benthopelagic, there were some that were bottom-dwellers. The following sketch illustrates the diversity of Silurian forms

Silurian Cephalopod modes of life

"A view of the mode of life of some Silurian nautiloids. In the top left a large orthoconic form [probably an Actinocerid or large Orthocerid; the shells of either of which reached a meter or more in length] swims forward, it's buoyancy nearly neutral and its hyponome bent back; its upper surface may have been camouflaged to allow the further possibility of a more concealed resting position on the sea floor, but these large nautiloids were at the top of the food pyramid and presumably had little to fear. The smaller orthoconic species below has remained undetected, its camouflage effective in the dappled light of the photic zone; it swims away backwards. In the bottom right a microphagous gomphoceroid [either an Oncocerid or a Discosorid, both independently evolved a very similar lifestyle and morphology] is suspended quietly in its vertical position; it would not have been obvious from above and may have had camouflage markings (not shown); in any case it could retract entirely within its shell. The cyrtoconic species [an Oncocerid] shown scavenging on the substrate has camouflage all round its shell; however its hyponome would permit swimming, when the cyrtocone would be brought to a more horizontal attitude. The torticonic *Foersteoceras*-like form is shown in its customary benthic position, though it could use its hyponome to direct an ascent through the water. In the upper right an *Ophioceras* is shown as a nimble and (unlike the large orthocone) highly maneuverable swimmer; it and the other forms are shown approximately to scale. Most streamlined and effective swimmer of all was the mature ascocerid shown above."

Drawing by Elaine Cullen, text by C.H. Holland [comments in square brackets by MAK]
from C.H. Holland, "Form and Function in Silurian Cephalopoda", 1984, *Special Papers in Palaeontology*, No,32, pp.151-164

Marginal Marine



A typical Silurian (Wenlock-Ludlow) vertebrate fauna from Saaremaa Island, Estonia. This fauna is dominated by agnaths, including thelodonts (1, *Phlebolepis*), heterostracans (2, *Toypelepis*), anaspids (3, *Rhyncholepis*), and osteostracans (4, *Procephalaspis*; 5, *Witaaspis*; 6, *Thyestes*; 7, *Dartmuthia*; 8, *Tremataspis*; 9, *Oeselaspis*). Jawed fishes are also present, especially acanthodians (10. *Nostolepis*) and possibly the earliest known osteichthyans (11. *Andeolepis,* known only from isolated scales and teeth). All these fishes lived in a marine environment, but osteostracans were more confined to lagoonal, shallow-water facies, whereas acanthodians and thelodonts were probably epipelagic.
Reconstruction and most of caption from Janvier 1996, p, 4

Estuarine biota

Lingulids, ostracods, eurypterids, limulids, scorpions, myriapods, trilobites, bivalves, agnathans, and possible also acanthodians were present or probably present in estuarine environments during the Middle and -Late Silurian (ref Devonian times - going upstream)

Eurypterids

Eurypterus remipes
Fiddler's Green Formation, Herkimer County, New York

from Dr Peter's Fossil Collection (former site)

"Eurypterids, an extinct group of aquatic chelicerates, were undoubtedly affected by environmental constraints imposed by their physiology and gross morphology, as are modern aquatic organisms. Kjellesvig-Waering (1961) proposed a series of distinct ecological phases for eurypterids, defined by the environment in which they lived, and based on the Upper Silurian Welsh Borderland fauna. However, evidence from the eurypterid fauna of the Upper Silurian Bertie Waterlime Formation, New York, suggests that two distinct transitional assemblages existed, perhaps caused by a difference in the environmental preferences of juvenile and adult eurypterids (‘ontogenetic segregation’) (Manning 1993). The eurypterids from the Upper Silurian of the Welsh Borderland may represent a previously undescribed, ontogenetically mixed, eurypterid assemblage, influenced by a series of facies changes; this is supported by sedimentological evidence (Manning, 1993). The distinct ecological phase model (Kjellesvig-Waering 1961) is rejected in favor of ecological gradients overlapping non-distinct eurypterid phases (inter-phase mixing). Inter-phase mixing might have been complicated further by the influence of ontogenetic migration of species across both physiological and environmental gradients. Combining this with new fossil evidence on the dual respiratory and osmoregulatory systems of eurypterids (Manning 1993; Manning & Dunlop 1995) leads to a better understanding of the palaeoecology of this enigmatic group" (Manning 1999).

Terrestrial

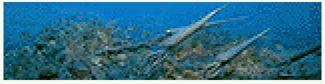
The most important evolutionary development of this period, was that of the first true terrestrial ecosystem

The first fossil records of vascular plants, that is, land plants with tissue that carries food, appeared in the Silurian period. They were simple plants that had not developed separate stems and leaves.

By the Middle Silurian, a very simple early terrestrial community with simple plant producers, millipede herbivores, centipede and arachnid carnivores, worm detritivores, and fungal decomposers had developed. The Mid-Late Silurian terrestrial biota included small plants along the water's edge, and arthropods such as trigonotarbids and myriapods (ref **Devonian Times -** going upstream). Fungi, nematodes, and perhaps earthworms were most likely present as well, although they did not leave a fossil record (except for possible fungi)

	LINKS	

The Silurian Period

 a Silurian reef by **The Virtual Silurian Reef** project

A good introduction to **the Silurian period** (complete with map) is included in the The Virtual Silurian Reef site.

Browse the Fossil Gallery - Silurian Period - a selection of Silurian fossils from Nova Scotia

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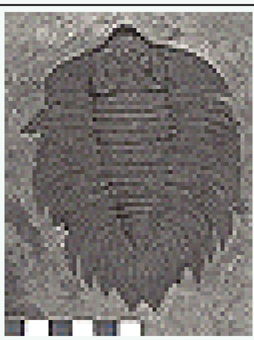
The Llandovery

The Llandovery Epoch of the Silurian Period: 444 to 428 Mya

Marine Invertebrates



Subclass Trilobita
Order **Lichida**
Family Lichidae

Arctinurus boltoni *(Bigsby)*

Horizon: Rochester Shale, Lewiston Member
Locality: Middleport, New York, USA
Size: (scale bar in cm)

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The Wenlock

The Wenlock Epoch of the Silurian Period: 428 to 423 Mya

During the Wenlock the oldest known tracheophytes (true land plants), of the genus *Cooksonia*, appear. The complexity of slightly younger (Ludlow) Gondwana plants like *Barragwanatha* indicates either a much longer history for vascular plants, perhaps extending into the early Silurian or even Ordovician, or else a misdating of the *Barragwanatha* sediments.

Stratigraphy

Epoch	stage	(page)	graptolite zone	English formation	Baltic Stratigraphic sub-zone
Wenlock	Homerian	latest	*Monograptus ludensis*	Wenlock	
				Tickwood	
		late	*Gothograptus nassa*		
		middle	*Crytograptus lundgreni*		

	Sheinwoodian	early			

Marine Invertebrates

Subclass Trilobita
Order Phacopida
Family Calymenidae

Calymene blumenbachi

Horizon: Wenlock Mudstone
Locality: near Wenlock Edge in Shropshire, England
Size: slightly over 5 cm long
notes: collected by Tom Levinson

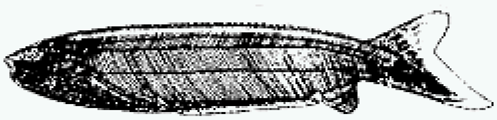
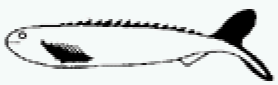
Subclass Trilobita
Order Phacopida
Family Calymenidae

Calymene cerebra

Horizon: Niagara Group
Locality: Wisconsin, USA
Size: (scale bar in cm)

Vertebrates

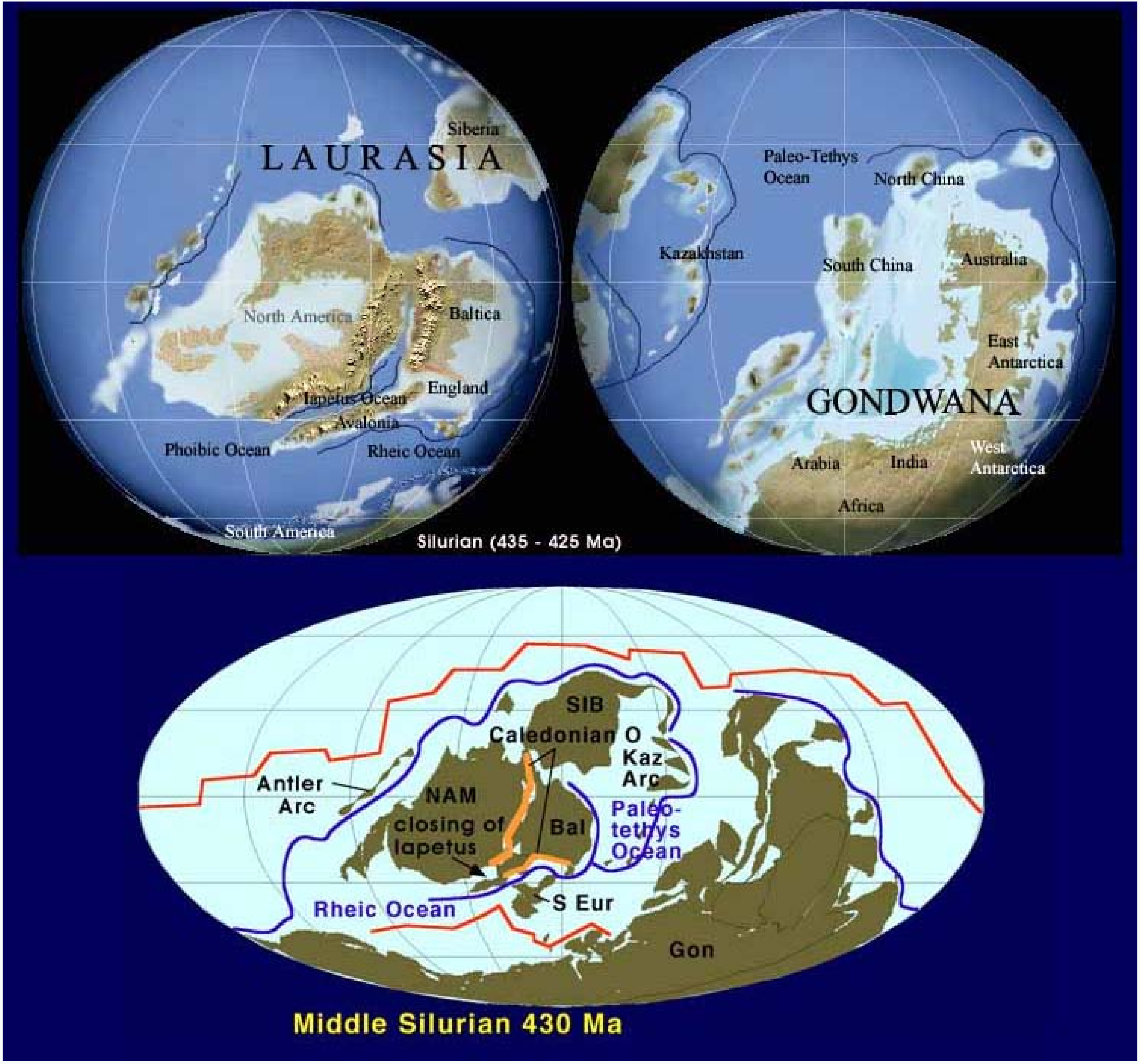
Jawless fishes

Class: Osteostraci	Class: Anaspida	
		
Ateleaspis	*Pharyngolepis*	*Lasanius*

Class Anaspida

The Ludlow

The Ludlow Epoch of the Silurian Period: 422 to 419 Mya



The Silurian World, adapted from the Paleogeographic Globes of Prof. Ron Blakey of Northern Arizona University

Geography of the Ludlow

The geography of the Ludlovian world is best known for the on-going train wreck which began the assembly of Laurasia -- or actually "Laurasia I" since there are arguably two continents by that name. By Ludlovian times, Baltica (including Scandinavia, European Russia and parts of Northern Europe) had collided with Laurentia (North America and Greenland). This began the north to south closure of the Iapetus Ocean which had previously separated the two. The western edge of Baltica was subducted under the Laurentian continent, with drastic effects in North America. These effects included the northern part of the Acadian Orogeny, a string of new volcanoes stretching from East Greenland (future home of *Ichthyostega* and other famous fossils) down the Laurentian coast towards New York and Pennsylvania.

In the meanwhile, the microcontinent of Avalonia, as well as bits and pieces of Southern Europe which had been flaking off the Gondwanan landmass, were running full tilt into the southern shores of Laurentia and Baltica. These fragments would add to what is now the lower eastern seaboard of the United States and Southern Europe, respectively. The exact timing of these events is not clear. Current thinking is that at least some of the European pieces arrived in Ludlovian times, but that Avalonia did not close the southern part of the Iapetus before the Pridoli, at the earliest.

Still further behind, Siberia was approaching the new Laurasian landmass from the northeast, followed by parts of what would eventually become Kazakhstan and Central Asia. The rest of the world looked much as it had since the beginning of the Cambrian, except that the entire Gondwanan landmass was continuing its slow slide across the South Pole which, in this era, passed through south central Africa. ATW

Ludlovian Climate and Environment

The Ludlow was a moderately warm era. The Ice Age which ended the Ordovician had long been over, although a small polar ice cap was probably still present in Africa. Oxygen had reached 50-100% of modern levels in the atmosphere, favoring the evolution of larger animals in suitable, shallow-water environments. There were a good many of these, since the Ludlow experienced the highest sea levels of the Paleozoic, and shallow seas covered many continental areas. Carbon dioxide levels were still quite high, perhaps 10 times today's concentrations. Indeed, carbon dioxide may actually have been increasing due to the extensive volcanic activity which accompanied the formation of Laurasia. The enormous Gondwanan peninsula formed by Australia and Antarctica prevented the formation of a continuous current around the South Pole, and the shores of the Gondwanan mainland were warmed by tropical waters flowing southeast through the Rheic Ocean. ATW

Marine Communities

The following diagram is a reconstruction of a late Ludlovian *Salopina Community* from W. S. McKerrow *The Ecology of Fossils*.

Silurian

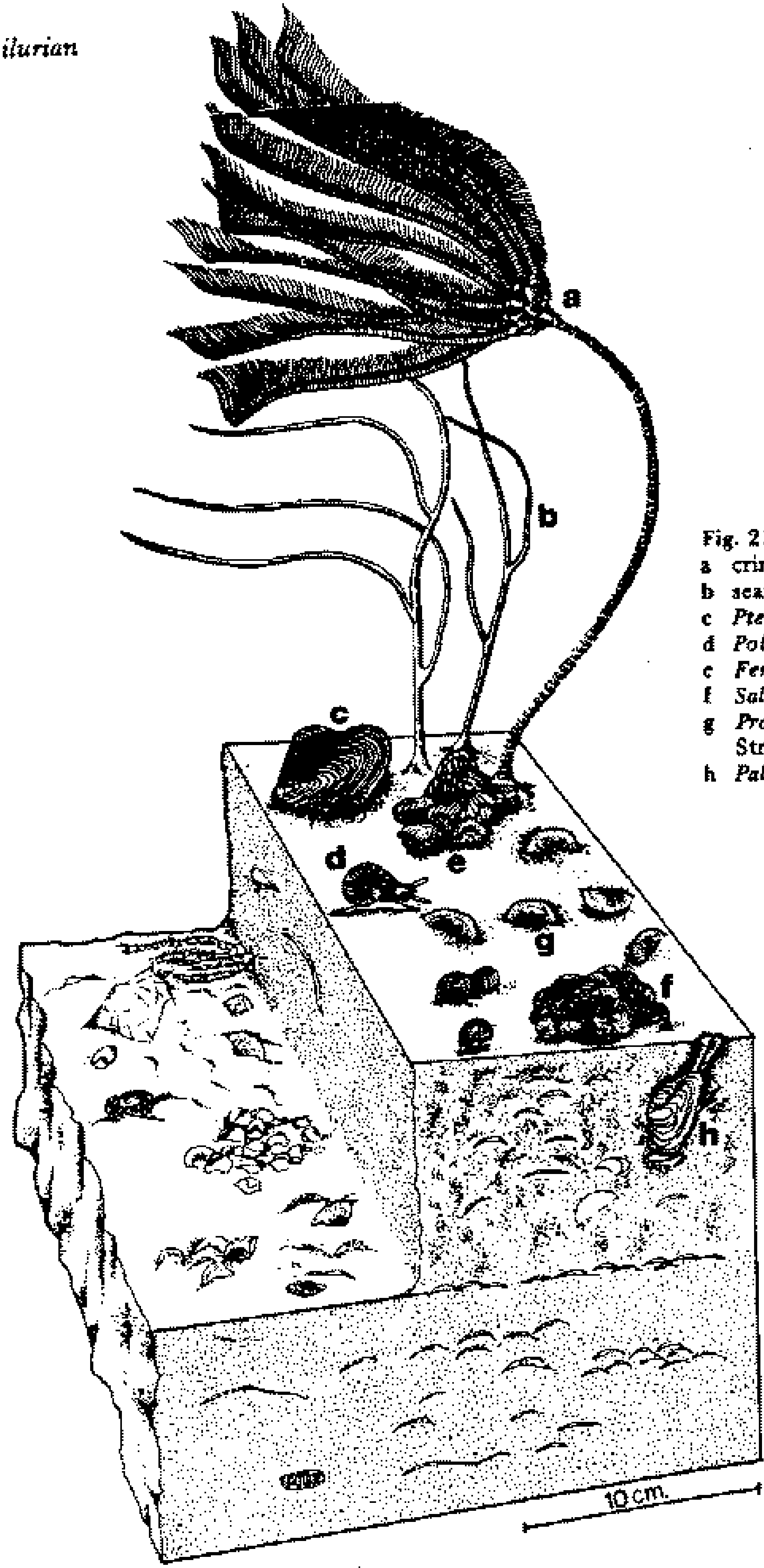
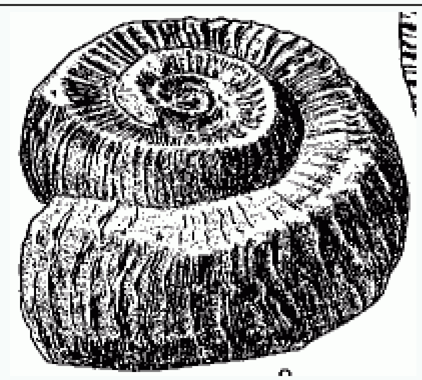


Fig. 21 Salopina Community

- a crinoid (Echinodermata: Crinozoa)
- b seaweed (Algae)
- c *Pteronitella* (Mollusca: Bivalvia: Pterioidea)
- d *Poleumita* (Mollusca: Archaeogastropoda)
- e *Ferganella* (Brachiopoda: Rhynchonellida)
- f *Salopina* (Brachiopoda: Orthida)
- g *Protochonetes ludloviensis* (Brachiopoda: Strophomenida)
- h *Palaeoneilo* (Mollusca: Bivalvia: nuculoid)

This is a shallow water marine benthic ecosystem that lived by the shore of the disappearing Iapetus Sea, Avalonia (see map, *above*, for global geography). Today this is the Welsh Borderlands. The *Salopina* Community succeeded the earlier *Eocolia* Community. The most common organism are suspension-feeding brachiopods and bivalves. Shown here are the brachiopods **(e)** *Ferganella*, a Rhynchonellid; **(f)** *Salopina*, an Orthid; and **(g)** *Protochonetes*, a primitive Productid; and the Bivalvia **(c)** *Pteronitella*, a Pterioid, and **(h)** *Palaeoneilo*, a nuculoid.

Protochonetes belongs to the Superfamily Chonetoidea, an ancestral group from which the rest of the Productida clade derived. So this was early and primitive member of a lineage that would become extremely important during the late Paleozoic. Productids are distinguished by the spines that protrude from the shell, anchoring it and allowing it to be raised above the sand and mud. This was an important ecological adaptation, because it reduced the possibility of fouling, and hence gave productids an advantage over other brachiopod groups.



Poleumita discors (Sowerby)
shell diameter about 5 cm
Wenlock to Ludlow age of Avalonia

Of other animals in this scene, Crinoids represent a higher tier of filter-feeders. The substrate consists of sand, or more fine-grained mud and silt. This was home to burrowing animals - worms, bivalves, trilobites, and others - as indicated by the bioturbation (disturbed mud). Gastropods are represented by the Euomphalid *Poleumita*, with a near-planispiral shell. A related species is shown at the right.

The same general area and age also yields a rare Silurian Lagerstätten, as indicated in the following report by Dr David Gladwell of the University of Leicester:

> "An exceptionally preserved biota of Upper Silurian (Ludlow Series) age is found in Lower Leintwardine Formation Channel fill deposits around Leintwardine in the Central Welsh Borderland. There are six submarine channels in total, although only four outcrop and yield fossil faunas...The fauna is diverse, containing common representatives of Silurian biotas (such as brachiopods and trilobites), along with more unusual forms such as ophiuroid and asteroid seastars, eurypterids, xiphosurids and phyllocarids....(T)he echinoderms are mostly complete, whilst the majority of the arthropod material is made up of disarticulated components. Specimens are predominately preserved as hard-parts, although occasional soft-body preservation is encountered in the form of rare 'worm' fossils. In addition to the dominant invertebrate fauna, relatively rare disarticulated components of heterostracan fish are found; the sole taxon found, *Archaegonaspis ludensis* (Salter, 1859) is the earliest known British species..."

MAK

Terrestrial Ecosystems

Even at this early date, the development of terrestrial ecosystems was well under way, as indicated by the following passage.

> "Sherwood-Pike and Gray (1985) describe probable ascomycete [this is unlikely! -- ATW] hyphae from Late Silurian (Ludlow) strata. They suggest that these were terrestrial Fungi at least contemporaneous with the earliest land plants. Some hyphae occurred inside small rounded pellets of apparent invertebrate fecal material; if this is correct, it suggests a fauna that included mycophagous (fungus-eating) microarthropods. Rolfe (1985b) accepts this suggestion and identifies millipedes from Late Silurian (Ludlow-Pridoli), now complemented by the discovery of predatory animals (Jeram et al. 1990). The importance these observations is that they confirm at least a minimal terrestrial food consisting of primary producers, decomposers, secondary consumers, and predators."

MAK

page by M. Alan Kazlev and ATW
page uploaded 10 June 2002
revised ATW030107 and MAK030427
(original uploaded on Kheper site 12 September 1998)
checked ATW031029

The Prídolí

The Pridoli Epoch of the Silurian Period: 419 to 416 Mya

Silurian Grammar

The Silurian Subcommission of the International Stratigraphic Commission was one of the first to complete its work. Holland (1985). Perhaps for that reason, among others, and for good or ill, the self-conscious internationalism of later reports was omitted. Consequently, some of the typographical conventions of the Silurian were retained. So, for example, The first epoh of the Silurian is the Llandovery, not the "Llandoverian." The Prídolí retains its original Slavic transliteration in the **Episodes** issue officially nominating the global stratotype section and point. Notwithstanding, it is usually written "Pridoli." We will use the two interchangeably and somewhat randomly.

The Prídolí remains the only epoch (series) which is not further subdivided into ages (stages). The current (2008) ICS scheme for the Carboniferous includes an additional *five* epochs with only a single age; but we have declined to adopt that usage.

Vertebrates

Hemicyclaspis

Land Plants

Assemblages containing *Cooksonia*, and other simple rhyniophytes are preserved in what were originally marine, nearshore, and occasionally in freshwater river deposits, at a number of localities around the margins of Euramerica (the so-called "Old Red Land "). Most fossils were of plants that had been transported by rivers away from the places where they grew, so their original habitats remain obscure. They are often associated with fragments of eurypterids.

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Joanna Snell, Wenlock Bryozoa from Wales and the Welsh Borderland (a poster presentation), Palaeontological Association, 43nd Annual Meeting, University of Manchester, 19-22 December 1999
referred to in ***Much Wenlock***

Rosanne Widdison, Biotic interactions in Wenlock Crinoidea (oral presentation), Palaeontological Association, 43nd Annual Meeting, University of Manchester, 19-22 December 1999
referred to in ***Much Wenlock***

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