j30 The Age of Marine Invertebrates (Early Paleozoic)

< mound reefs, plankton, suspension feeders, invertebrate scavengers >

When challenged by a zealous Popperian to say how evolution could ever be falsified, J.B.S. Haldane famously growled: 'Fossil rabbits in the Precambrian.' —Richard Dawkins.[1]

During the Early Paleozoic the sterility of the land stood in the starkest contrast with the oceans where abundant, and varied, invertebrate life flourished:[2]

Reef builders and benthic faunas

Late Cambrian reef-framework building invertebrates were stromatoporoids, tabulate corals, and bryozoans. The Sauk seafloor was also inhabited by a variety of brachiopods and sponges.

Articulate brachiopod species are comparatively numerous today and inarticulate brachiopod species are few. This bias was set by the end of the Devonian before which articulate brachiopods had diversified and inarticulate brachiopods had dwindled from the inception of these classes in the Cambrian when the bias was the reverse (***Figure j30.1***). Bryozoans are always found in association with the brachiopods and their variety has been in concert. The bryozoan heyday was in the Late Devonian when clastic limestones are commonly mostly of their remains.

Sponges (some 15,000 species are extant and many are a source for therapeutic drugs) are remarkable for totipotency (the ability of a cell to differentiate into other cell types) and plasticity of form. Sponges are with cells that secrete skeletal elements called *spicules*. Some sponge varieties, the Archaeocyathids, were already dwindling to become extinct for unknown and unknowable reasons soon after the end of the Lower Cambrian. Their calcareous shells were double walled and vase shaped. Their variety was to more than 450 species (assigned to 92 genera, 26 families, and 8 orders). Some species grew in such profusion that they built submerged reefs (Labrador, Virginia, California, and Australia) in what are interpreted to have been in shallow, warm, equatorial waters. Archaeocyathids (their name means "ancient cup") are a type fossil for the Lower Cambrian.

Acritarchs (phytoplankton)

Given the presence of suspension feeders and the occurrence of these in shallow-water sediments, the base of the food chain would have been, as today, planktonic plant protista (singled celled photosynthetic organisms). Species of such, at the time of their existence, are never rare but only those with hard parts may leave direct evidence of their nature.

Existing marine phytoplankton groups, such as the radiolaria and diatoms, appeared just before the beginning of the Cenozoic, and dinoflagellates and the coccolithophores appeared at the beginning of the Jurassic. Enigmatic forms of extinct fossilized phytoplankton that are clearly not those of living types are assigned to the acritarchs. Acritarch is a catch-all name, proposed in the Downie-Evitt-Sarjeant classification, 1963, for resistant-walled, possible, phytoplankton comparable in their size and form to extant phytoplankton such as dinoflagellates that when encysted have a body wall that is resistant to decomposition.[3] Acritarch tests are smooth to spiny. Acritarchs dwindled to small variety during the Early Mesozoic having begun their decline during the Late Paleozoic. Acritarchs, abundantly fossilized in Lower Paleozoic marine strata, first appeared in the Cambrian.

Ostracods

Shelled ostracods (tiny bivalve invertebrates) are an important component of the aquatic food web today. Their some 33,000 living and extinct species have a variety of shell shapes valuable for biostratigraphy. As for their soft parts "these guys have just been plodding along totally unfazed." remarks Tom Cronin.[4] The evidence is 5-centimeter-long *Colymbosathon ecplecticos* from Herefordshire, U.K., where marine animals buried in 425-million-year-old volcanic ash were mineralized rapidly enough to have their soft parts preserved in three dimensions within nodules, These, unintentional voyeurs David Siveter, Derek Siveter & Mark Sutton, and Derek Briggs, working separately, flat-grind away and photograph polished cross sections that are then assembled. Six pairs of gills help pin Silurian *C. ecplecticos* to the yet extant family Cylindroleberididae. Also noted of it are: limbs for sensing, feeding, and swimming; a "furca," probably used to grasp prey and carrion; and, a stout (and oldest on record) copulatory organ. Appropriately, the creature's name is Greek for "amazing swimmer with a large penis." Ostracods debuted in the Cambrian.[5]

Graptolites [6]

The graptolites, extinct at the close of the Mississippian, had chitinous hard parts. Their remains are best preserved where they came to litter the bedding planes of dark shales which were accumulating in deep water and under anaerobic conditions. The name graptolite means written on stone. This is descriptive because carbonized remains of graptolites look like pencil marks. The marine facies, in which graptolites are guide fossils, is called the "graptolite facies" which contrasts with the coeval shallow, well-oxygenated marine "shelly facies" (clastic carbonate) wave-disturbed (high-energy) seafloor environments in which graptolites are little preserved. Graptolites are of two orders:

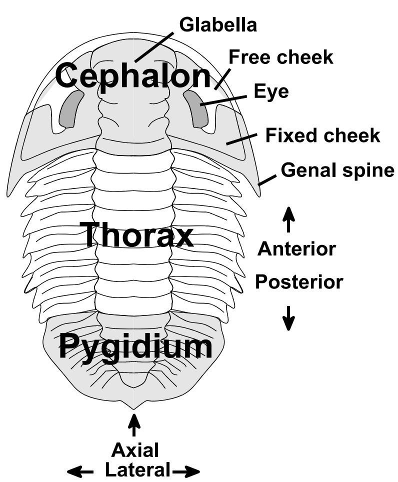
Graptoloid graptolites (graptoloids) were all floating colonies. Parallel evolutionary trends, presumably in response to a globally changing ecology, is a feature of separate lineages of graptoloids. Pelagic graptoloids are guide fossils for Silurian and Ordovician strata.

Dendroid graptolites (dendroids) grew as bush-like colonies attached to the seafloor. One species, *Dictyonema flabelliforme*, which either had a float or lived attached to drifting seaweed, achieved a worldwide distribution and is guide fossil for the earliest Ordovician.

Graptoloids appeared at the beginning of the Ordovician, and the less-derived dendroids appeared earlier, near the end of the Cambrian.

Trilobites

The trilobites, extinct at the close of the Paleozoic, had dwindled (while fishes flourished, by contrast) to a last few stragglers in the Permian from their Early Ordovician and Late Cambrian heyday. Trilobites were in existence for 300 million years, having appeared (with many legs for scrabbling detritus for morsels, and with mouth parts that enabled weak chewing) near the beginning of the Cambrian as the first hard-shelled macroscopic invertebrates.



In concert with the rise of fishes, trilobite adaptational trends had been to greater mobility and, for effective swimming, a more streamlined body-outline and eyes to the side of the cephalon. Some species could have had an entirely nectonic life style. The number of genera in association with fishes and cephalopods in the Carboniferous were less than a dozen genera. This is in the greatest contrast with trilobite's earlier history recorded in Ordovician and Cambrian marine strata. At many horizons in these, are found numerous, distinctive, short-ranged trilobite species. The rise of the nautiloid cephalopods during the Ordovician from their first appearance in the Upper Cambrian was not matched by a decline of trilobite diversity. The rate of trilobite speciation was rapid as evidenced by a simple count of thousands of species allocatable into hundreds of genera at the end of the Cambrian. At the beginning of the Cambrian, a count of 600 recognized genera were more but, at this time of first appearance of shelled trilobites, the number of species were fewer.

Gradualistic evolution of trilobite species in one layer into forms in the next is not found and trilobite evolution is a prime example of "punctuated evolution" (Eldredge and Gould's name for the mechanistic explanation of that aspect of the fossil record—characterize by detractors as "evolution by jerks"— or otherwise, Gould countered, "evolution by creeps").[7] Allison R. Palmer in 1956 proposed the term *biomere* for a biostratigraphic unit that is "bounded by abrupt nonevolutionary changes in the dominant elements of a single phylum." [8]

Compared to their nectonic-adapted descendants, trilobites during their Ordovician and Cambrian heyday had comparatively small eyes atop the cephalon, and a large number of thoracic segments.

Their life style as crawling scavengers and mud processors, is indicated by their mouth underside the cephalon, and by the trace fossils they left of their scrabblings and diggings. Some were infaunal, and some tiny ones, the agnostids, were planktonic. Some trilobites useful as guide fossils are also facies fossils. For example in the Laurentian geocline (exposures in Pennsylvania, New York, Vermont, Newfoundland Greenland, and Scotland), *Olenellus* (Lower Cambrian) inhabited turbulent, well oxygenated, shallow seafloors (North American Faunal Province) and *Holmia* (Lower Cambrian), inhabited muddy or silty deep seafloors (European Faunal Province) (***Figure j30.2***).[9]

Sensitivity to their place in the developing ecology is suggested by trilobite diversity characterize by boom and bust (rapid radiation following abrupt extinctions). Cambrian biosomes, with 40 to 90 percent replacement of trilobite species in each, are useful for stratigraphic subdivisions. The term *biosome* was coined by Harry E. Wheeler in 1968 for an ecologically controlled biostratigraphic unit that intertongues with strata to either side that can be of different sedimentary-rock type to it and to each other.[10]

Echinoderms

Echinoderm species, though greatly varied in form since the Cambrian, are relatively easy to assign to relatively few classes of the phylum. None however show any clear relationship to any species that were evolving during the Cambrian. Then a variety of strange plated forms, considered to be echinoderms, are species so different from each other that they are assigned to different classes, each with one, or only a few, genera.

Conodonts

Conodonts are tiny, 0.3 to 1.5 mm in length, typically light brown, glassy in appearance, toothlike fossils that can be extracted from almost all marine shales and limestones older than Upper Triassic, to as far back as Middle Cambrian. The name conodont means "cone tooth." which describes their general appearance. They are greatly varied from spiky to comblike to bladelike, and suites of distinctive conodonts have proven to be excellent guide fossils.

Conodonts are composed of apatite (calcium phosphate). They are extracted by washing separation (elutriation) from clays, or crushed shale, or are freed as residues by acetic-, monochloracetic-, or formic-acid solution of limestones and dolomites. The conodont apatite is crystalline, fibrous or finely laminated, translucent, and yellow to brown in color. Their color most easily distinguishes them from scolecodonts (silicochitinous teeth of annelid worms) that are similar in general morphology but which due to carbonization occur as jet-black fossils.

Conodonts, so named in 1856 by Christian Heinrich Pander who first described and illustrated them believing them to be teeth[11] (which turns out to be correct), remained mere curiosities until Edward Oscar Ulrich and Ray Smith Bassler in 1926 demonstrated the utility of these microfossils (common in well cuttings) in solving stratigraphic problems.[12] Just what conodonts were was long a mystery (now solved). Different shaped conodonts in arrangements each of which indicates one animal had been found. However, save for shape pairs, that information is lost by the way conodonts are usually obtained. But for biostratigraphic determinations their use for a nuts-and-bolts procedure is not compromised. Also reasonable, is classification of conodonts by numerical taxonomy methods.

Pander, who considered conodonts to be the teeth of fish, confessed that he could not determine from what parts of the mouth the several different forms came. Speculation as to their true nature, by others, did not favor the possibility that they are teeth. Opinions were also as to whether they were parts of vertebrates or invertebrates. In 1953, in *Principles of Invertebrate Paleontology*, Robert R. Shrock and William H. Twenhofel mention that "There is a certain humorous aspect to the fact that vertebrate paleontologists rather generally brush aside the idea that Conodonts are vertebrate remains, whereas the invertebrate paleontologists, vigorously insisting that they are vertebrate remains, quickly become conservative and argumentative if the tables be turned by some colleague who suggests that they may be invertebrate remains."[13] Finally, Euan N. K. Clarkson in 1982 spotted a lamprey-like conodont animal in a museum drawer of fossils, and by 1983, D. E. G. Briggs had described it. Its soft parts were fossilized as bedding-surface impression in a slab of Late Paleozoic shale. The animal is an eel-like swimming vertebrate (bilateral body) with a mineralized exoskeleton, a caudal fin with radials, and the conodonts are in the head region where teeth should be.[14]

In 1995, Sarah E. Gabbott described the fossil of a giant conodont, *Promissum pulchrum*.[15] From this fossil, Mark A. Purnell in 1995 could describe distinctive eye muscles (as exist only in vertebrates) to which would have attached externally two bulging eyes. The muscles would have allowed the conodont to shift its lustrous gaze beguilingly (but, if so, unappreciated by evolving fish) up and down and from side to side.[16] Also (fascinated by teeth, by the personal distinction admitted of being born without any)[17] he found that not only do conodonts' conodonts look like teeth but show in electron microscope images, etched pits and wear scratches of exposed and used teeth. These conodonts had crushed and sheared food. The degree of tooth abrasion indicates a predatory animal that devoured fairly large prey. (Although the name conodont does mean cone-tooth, paleontologists using optical microscopes had previously discounted the resemblance because they had seen no signs of wear.)[18]

The conodonts are extinct vertebrates. How they fit into the classification of the vertebrates in general should be considered. Animals with a skull and sensory capsules are called *craniates*. These range from hagfish to elephants (which is to say from jawless fish, through armored jawless fish, to jawed vertebrates).[19] Philippe Janveir considers that the conodonts can be placed, in their affinities, just before or among "ostracoderms" (a grab-bag of extinct Paleozoic armored jawless vertebrates).[20] That conodonts were hard teeth of a soft bodied predator/scavenger, allows Purnell in 1995 to suggest that the vertebrate skeleton evolved first to enhance active feeding (recall the secondary pallet of crocodiles) and did not evolve first for protection against predators as Romer surmised in 1933.[21] ❑

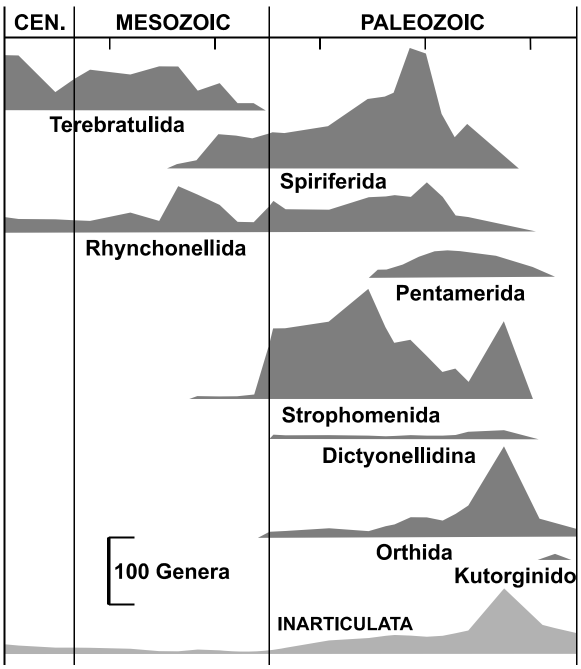


Figure j30.1 **Ranges and diversity of the Brachiopods**
Key: articulate orders (dark gray), inarticulates (pale gray)

Figure j30.2 [22] **Cambrian faunal provinces on both sides of the North Atlantic Ocean**

The "American" (black areas) occurs chiefly in shelly carbonate rocks of the Sauk epeiric sea on Laurentia and the "European" (gray areas) fauna characterizes graptolite-bearing shales, of the deep water outer part of the passive Laurentian geosyncline. The boundary was found to be narrowly gradational where the two faunas mixed in the same strata in western Newfoundland and elsewhere. The match between these faunal provinces, either side of the Atlantic, was evidence that early supported the theory of continental drift.