The first complex ecosystems

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Today's ecosystems are amazing in the complexity of the interdependent relationships between the organisms that make up them. Energy and biomass circulate through food webs that unite bacteria, unicellular organisms, plants/algae and animals of extremely varied nature and size. The stability of these biological systems is based on dynamic balances that are nevertheless very sensitive to environmental and anthropogenic factors. For more than three billion years, marine ecosystems have been dominated by microbial organisms (bacteria, archaea) or unicellular eukaryotes. While these organisms have played a key role in the biogeochemical cycles of carbon or nitrogen and in raising the level of oxygen on our planet, they have never formed complex food webs as we know them in nature today. A little over 500 million years ago, the appearance of multicellular and macroscopic organisms at the end of the Precambrian and the advent of the animal kingdom during the Precambrian-Paleozoic transition revolutionized the marine world and its mode of operation.

1. The enigmatic marine ecosystem of the Ediacaran

Figure 1. Typical organisms of the Terminal Precambrian (Ediacaran) marine ecosystem (a) Sling-shaped rangeomorph colony anchored to the bottom by a long stem; bench area of the Mistaken Point deposit, Newfoundland, Canada. (b) Reconstruction of a rangeomorph showing the fractal structures of the slingshot. (c-f) White Sea Fauna, Russia; respectively, undetermined form, Dickinsonia, Kimberella, Archaeaspis. Scales: 10 cm in (a), 1 cm in (c-e) and 5 mm in (f). [Source: M. Laflamme (a), Narbonne et al. 2009 [see ref. 1] (b) and J. Vannier (c-f)]

Completely new organisms appear in the marine environment at the end of the Precambrian. They are distinguished by their large size (from several centimetres to about a metre; never achieved before) and by their unprecedented architectural complexity (Figure 1).

Present in many fossil sites in Canada (e.g. Mistaken Point), Australia (e.g. Ediacara), Namibia and northern Russia (e.g. White Sea), these enigmatic organisms have colonized the seabed in abundance at variable depths between 575 and 542 million years, a geological interval corresponding to the end of the **Ediacaran**. The footprints of their soft, fleecy and flexible bodies, without equivalent in today's nature, have been preserved thanks to the instantaneous deposition of sandy sediments or volcanic ash.

Among the most typical, **rangeomorphs** [1] are characterized by a wavy frondo{ind-text}Structure of a flattened, relatively large, leaf-like living organ or organism.{end-tooltip} with a stem firmly anchored to the bottom. These fixed organisms, unique in their modular and fractal structure, do not, however, reach the anatomical complexity of the first Cambrian animals. Apparently devoid of mouth, digestive system and complex internal organs, they were thought to have extracted their food by direct absorption of dissolved organic carbon (osmotrophy{ind-text}A mode of feeding that consists of feeding from dissolved substances. The osmotrophic organisms are nourished by transmembrane exchange, *i.e.* by diffusion of ions or small molecules through the cytoplasmic membrane. This type of nutrition, which is very common among microorganisms, is also provided by a number of animals, both free and parasitic. It is only possible in liquid environments (aquatic environments, internal fluids of animals or plants) or by the synthesis of enzymes that "digest" their solid environment.{end-tooltip}) thanks to their very large surface of exchange with the environment.

At the Ediacaran, the water-sediment interface of the ocean floor was also occupied by **sponges** and many flattened organisms sometimes evoking the bilateral symmetry of some molluscs{ind-text}Embranchement of invertebrate animals, not segmented, with bilateral symmetry sometimes altered. They have a soft body (hence the name mollusk) usually composed of a head, a visceral mass, and a foot. They may have a calcareous shell produced by a mantle covering the visceral mass. {end-tooltip} and current arthropods{end-text|width=200}Branch of invertebrate animals whose organisational plane is characterised by a body segmented with articulated appendages and covered by a rigid cuticle or shell, which constitutes their exoskeleton, in most cases composed of chitin. The arthropod branch appeared 543 million years ago and is by far the one with the most species and individuals in the entire animal kingdom (80% of known species).{end-tooltip} (Figure 1). Traces produced by some of them such as *Kimberella, Dickinsonia and Yorgia* indicate that they moved and consumed the bacterial films{ind-text} Also called biofilms; microbial community marked by the secretion of an adhesive and protective matrix. It is usually formed in water or in an aqueous medium. Biofilms were probably the first colonies of living organisms more than 3.5 billion years ago. With stromatolites, they seem to be the origin of the first biogenic rocks and reef structures{end-tooltip}, which then covered the entire seabed, probably by external digestion along their ventral surface as in the placozoaires{ind-text}Metazoans (animals) with the simplest organizational plan. These tiny (between 1 and 3 mm) flattened animals have no symmetry, no mouth, no digestive tract, no nervous system, no basal blade. They have no organs and only four different types of somatic cells. The vast majority of Ediacaran organisms appear to belong to evolutionary lines that appeared before those of animals in the strict sense (Eumetazoaires{end-text}Higher (animal) metazoans including all major animal groups except sponges and placozoa.{end-tooltip}).

The marine ecosystem of that time was essentially dominated by **microbial mats** and **osmotrophic** multicellular organisms (e. g. rangeomorphs), microphages{ind-text}Animals consuming very small amounts of solid food (particles) that must be absorbed in large quantities. The particles ingested range from organic debris a few nanometres in size to shellfish and shrimp. This is an important part of the krill on which whales feed{end-tooltip} (e.g. sponges via their filter system and their flagellated{ind-text}characteristics of unicellular cells or organisms equipped with one or more flagella, structure ensuring their mobility.{end-tooltip} cells) or using external contact digestion. These feeding strategies were perfectly adapted to the resources available in the marine environment at the end of the Precambrian, namely an abundant flow of dissolved organic matter and microbial mats ubiquitous at the water-sediment interface. The extinction of Ediacaran organisms at the Precambrian-Cambrian transition would not be due to a global environmental upheaval like most major biological crises, but rather to the destruction of their biotope{ind-text}Location with relatively uniform determined physical and chemical characteristics. This environment is home to a set of life forms that make up biocenosis: flora, fauna, micro-organisms. A biotope and the biocenosis it supports form an ecosystem.{end-tooltip} by the very first burrowing animals (bioturbation{end-text}Active mixing of soil or water layers by living species, mainly animals.{end-tooltip}). Completely defenceless, these organisms would not have survived the first predators.

2. The first animal communities: prototype of modern ecosystems

By definition, **Cambrian Explosion** refers to the relatively sudden appearance in the fossil record of both new and anatomically complex organisms, among which we can certainly recognize the distant ancestors of the main current animal groups (e. g. arthropods, worms, molluscs, chordates; Figure 2). Several exceptionally preserved deposits (called Lagerstätten{ind-text}German word, plural, literally meaning "storage area". Corresponds to geological sites of extreme fossil richness that have been remarkably preserved ({end-tooltip}) such as Chengjiang (China; approx. 520 Ma), Burgess Shales (Canada; approx. 505 Ma), Sirius Passet (Greenland) and Emu Bay (Australia) reveal the existence of the first marine animal communities. Thanks to already developed motor and sensory capacities (e.g., sometimes fossilized cephalic nervous system), these early Cambrian animals were able to move actively in their environment and exploit for the first time a multitude of ecological niches. This dynamic marks a fundamental difference with the essentially fixed marine life of the Ediacaran and an irreversible turning point in the evolution of **ecosystems**.

Figure 2. Cambrian animals from exceptionally preserved deposits. (a) Wiwaxia, a primitive mollusc protected by sclerites. (b) Cricocosmia, a worm close to priapulans (worms in the shape of a small penis) protected by a series of plates. (c) Ottoia, a priapulan worm showing its evaginated pharynx (left) and food remains in its intestine (right). (d) Paucipodia, lobopodian, primary arthropod with non-articulated appendages (e) Hallucigenia lobopodian considered as an ancestor of the current onychophores, carrying thorns on its back. (f) Anomalocaridae (juvenile) showing powerful prehensil appendages. (g)-(i) Sidneyia, emblematic arthropod of the Burgess Shale; general view, intestinal contents (trilobites) and details of the chewing appendages. (j) Waptia, an arthropod with a flexible abdomen. a, c, e, e, g-j come from the Burgess Shales (British Columbia, Canada); b, d, f from Chengjiang (Yunnan, China). Scales: 1 cm in a, c, d, f-h; 5 mm in b, e, i; 1 mm in h. [Source: © J. Vannier, except e (J.-B. Caron)].

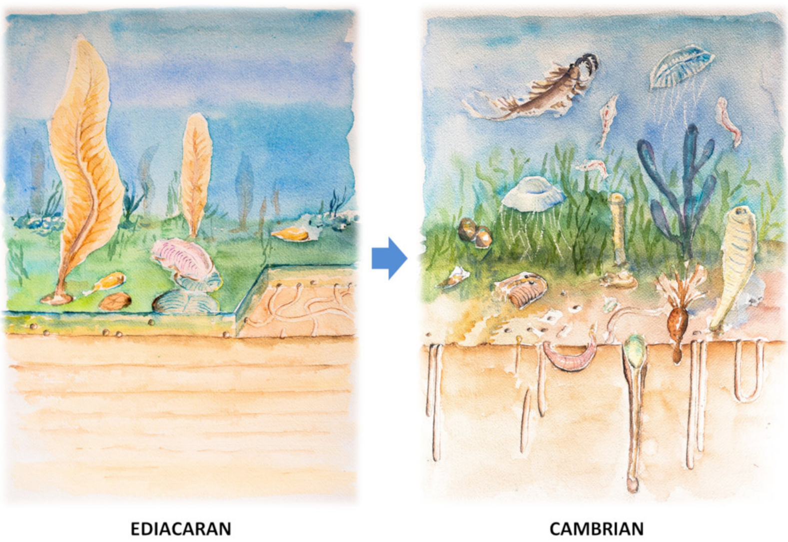

Figure 3. Transformation of the seabed at the Ediacaran-Cambrian transition due to increased bioturbation within the sediment and decline of microbial mats. Watercolour by Richard Bligny, inspired by Fedonkin et al. 2007 (see ref. [2]).

From the beginning of the Cambrian, many worms close to the priapulans{ind-text}in the shape of a small penis.{end-tooltip} [2] colonize the interior of current sediments. Long sealed and laminated by microbial mats, the seabed is disturbed by the increasingly intense and deep burrowing activity of these worms (Figure 3) [2]. This event, sometimes referred to as the "Agronomic Revolution", creates new habitats and resources and modifies the redox gradient{ind-text}Chemical gradient between oxidized and reduced molecules.{end-tooltip} through the sediment. Some priapulan worms (e.g. *Ottoia*) captured a wide variety of small animals living on the bottom (e.g. hyoliths, other worms, small arthropods) thanks to their evaginable{ind-text}Who protrudes externally.{end-tooltip} pharynx with teeth, as shown in the study of their intestinal contents. Totally unknown in the Precambrian, **predation** thus appears within Cambrian marine communities.

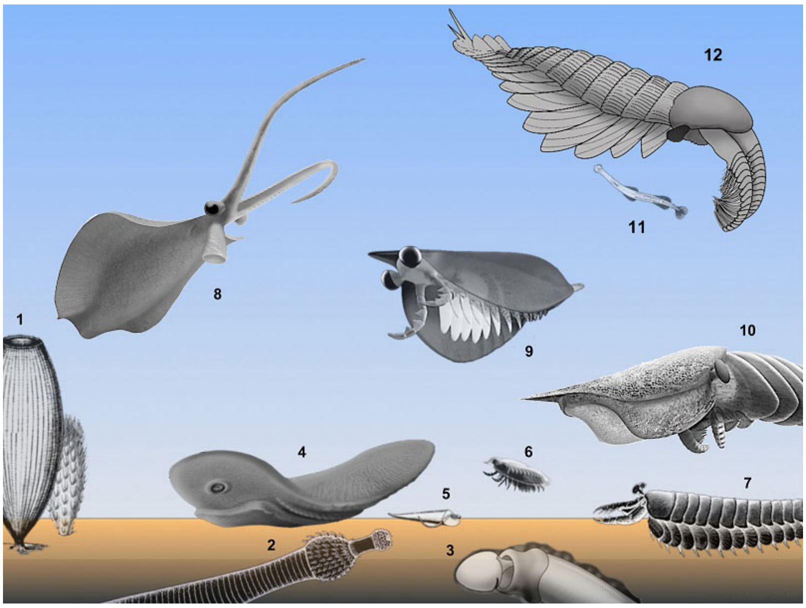

Figure 4. Schematic representation of Cambrian communities. 1, sponges; 2, Ottoia (predatory priapulan worm); 3, Spartobranchus (tubular enteropneuste); 4, Odontogriphus (primitive grazing mollusc); 5, hyolite; 6, bradoriid arthropod; 7, Fortiforceps (arthropod with prehensil frontal appendages; 8, Nectocaris (primitive swimming mollusc); 9, Isoxys (swimming arthropod); 10, Hurdia (predatory anomalocaridae); 11, chaetognathe (predatory planktonic organism); 12, Tamisiocaris (filter appendages anomalocaridae). [Source : J. Vannier; simplified drawings from Briggs et al. 1994 [3] ; Caron et al. 2006 [4]; Caron et al. 2013 [5]; Daley et al. 2009 [6]; Hou et al. 2004 [7]; Smith and Caron 2010 [8]; Vannier 2012 [9]; Vannier et al. 2007 [10], 2009 [11]; Vinther et al. 2014 [12]; http://www.burgess-shale.rom.on.ca/]

In parallel, the water column{ind-text}Volume of water above the bottom.{end-tooltip} above the sediments is populated by a multitude of swimming animals such as:
- cnidarians{ind-text}A branch (phylum) of aquatic animals (mainly marine) that is found in two forms: polyps, when fixed (as in the case of coral or sea anemones), and jellyfish when they are swimmers.{end-tooltip},
- ctenophores{ind-text}Small, hermaphroditic, predatory marine organisms. They have a vague similarity to jellyfish and are a very important part of the plankton,
- chaetognates{ind-text}A branch (phylum) of arrow-shaped marine predators named after the mobile hooks that capture their prey. They play a major role in the planktonic ecosystem as the main direct predators of copepods and represent up to 10% of the zooplankton biomass.{end-tooltip},
- primary molluscs and arthropods (e.g. Isoxys{ind-text}Extinct type of small primary arthropods that lived in the Lower Cambrian. Their main characteristic is the existence of a pointed bivalve shell.{end-tooltip}).

The comparative study of these fossils and their current descendants (Figure 4) suggests that the species interacted within a primitive **food chain** [3],[4],[5],[6],[7],[8],[9],[10],[11]. The Lower Cambrian *Timisiocari* species of Greenland is a good example of these new trophic relationships. Close cousin of the emblematic predator *Anomalocaris*, its large appendages were equipped with combs and filter bristles allowing it to catch zooplankton{ind-text}Animal plankton. It feeds on living matter, some species being herbivores and others carnivores.{end-tooltip} living in suspension in the water column. Microfossils attest to the presence of this zooplankton that consumes eukaryotic algae and bacteria.

However, Cambrian marine life is concentrated at the water-sediment interface, with sponges representing a major component of sessile fauna{ind-text}Organizations living alone or in colonies and permanently fixed directly to the substratum. They are most often aquatic. This is the case, for example, for sponges, corals, hydrozoa, tunicates, bryozoans, etc. {end-tooltip}. **Arthropods** are by far the most abundant and diverse epibenthic organisms{ind-text} Organisms living on the surface of the bedrock in the seabed area. {end-tooltip} in all deposits with exceptional preservation (Figure 2). Their external (segments, appendages) and internal (nervous system) organization plan suggests, for some of them, kinship relationships with current crustaceans and chelicerates{ind-text}Group of arthropods carrying chelicera, a pair of appendages close to the mouth, corresponding to the second pair of antennas in mandibules (crustaceans, insects...). This group includes merostomes (limules) and arachnids (spiders, scorpions, etc.). Only the horseshoe crabs are marine animals and live on the bottom.{end-tooltip}.

Others belong to groups that are now extinct. Their articulated and multi-segmented exoskeleton has probably favoured the acquisition of many functionalities and specializations. Prehensil and chewing appendages allow Cambrian arthropods to capture prey and reduce food particles. **Macrophagia** appears in Cambrian times in many predatory animals or animals that feed on corpses (scavengers). For example, the *Sidneyia* arthropod of the **Burgess Shale** captured, crushed and consumed small trilobites{ind-text}A class of fossil marine arthropods that existed during the Paleozoic (primary era) from Cambrian to Permian. The last trilobites disappeared during the mass extinction at the end of the Permian, there are 250 Ma.{end-tooltip} as indicated by its appendages and stomach contents (Figure 2).

Other innovations contribute to the major changes in the food chain. Digestive glands increase the efficiency of enzymatic degradation of food, thus promoting macrophagia{ind-text}Mode of nutrition of a living organism that feeds on large prey compared to it. {end-tooltip} in many arthropods in Cambodia. The vision also revolutionized the interactions between marine organisms from the early Cambrian period. Thus, large compound eyes made up of thousands of facets allowed the super-predator *Anomalocaris* to spot and track its prey. There is no doubt that vision, widespread among Cambrian arthropods, has significantly altered prey-predator relationships and introduced new selection pressures within the ecosystem, leading to multiple adaptive responses.

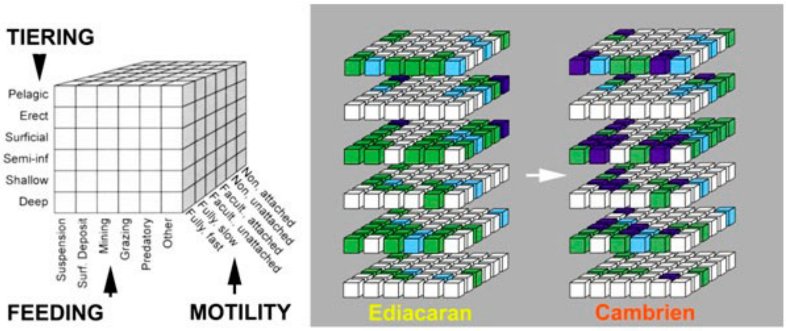

Figure 5. Complexification of the marine ecosystem at the Precambrian-Cambrian transition visualized by a theoretical three-axis eco-space (tiering, food pattern and mobility of organisms) containing 216 cubes that represent possible lifestyles (only 118 of which are ecologically sustainable). On the right, the comparative filling of the Ediacaran and Cambrian eco-space according to palaeontological data. In green and blue: lifestyles identified in current ecosystems (corresponding to 92 out of 118 cubes). In purple: lifestyles identified in the Ediacaran and Cambrian, they represent about 10% of potential lifestyles; their number increases significantly between the Ediacaran and Cambrian. [Source: Simplified from Bambach et al. 2007 [12] and Erwin & Valentine 2013 [13].]

Although it is clear that a complex prototype trophic web{ind-text}Describes some species relationships (predator-prey relationships in particular), energy and nutrient cycles and flows within ecosystems between producers, consumers and decomposers. The basic level of this network is that of autotrophic primary production, above this level, each link in a food chain corresponds to a complex trophic level. {end-tooltip} is established from the Lower Cambrian, it remains very difficult to quantify interactions between organisms as it is possible to do for current **ecosystems**. Few quantitative approaches compare Precambrian, Cambrian and current ecosystems. However, the construction of a three-dimensional representation of a theoretical ecosystem according to three axes (tiering, food mode and mobility of organisms) [12].Theoretical three-axis representation of a theoretical ecosystem according to three axes (tiering, feeding mode and mobility of organisms) allows us to visualize the occupation of **ecological niches** at different periods of geological time (Figure 5) [12],[13]. We can thus see a filling of the eco-space at the Precambrian-Cambrian transition, which will intensify in the Ordovician during the great Ordovician biodiversification event{ind-text}Period in the history of the Earth during which the biodiversity of oceanic life has increased the most. It occurs about 40 to 80 million years after the Cambrian explosion. Its duration is of the order of 25 million years (a relatively short interval on the geological time scale), and is located during the lower and middle part of the Ordovician system, dated between 485 and 460 million years.{end-tooltip}, to finally give the marine world the appearance and operating principles we know it.

References and notes

Cover image. *Life in the Ediacara Sea* [© Ryan Somma (CC BY-SA 2.0), via Wikimedia Commons]

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