

Paleobiology

Information landscapes and sensory ecology of the Cambrian Radiation

Roy E. Plotnick, Stephen Q. Dornbos, and Junyuan Chen

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Abstract.—Organisms emit, detect, and respond to a huge array of environmental signals. The distribution of a given signal is dependent, first of all, upon the original spatial distribution of signal sources, the *source landscape*. The signal sources can be fixed or moving and their output can be stable or ephemeral. Different sources can also occupy the same general spatial location, such as insects living on a host plant. The emitted signals are modified by relevant transport processes, which are often strongly scale and environment dependent. Chemical signals, for example, are propagated by diffusion and turbulence. The resulting complex, three-dimensional, and dynamic distribution of signals in the environment is the *signal landscape*; it is the environment of potentially available information in which sensory systems function and have evolved. Organisms also differ widely in what signals they can actually detect; the distribution of signals that an organism can potentially respond to is its *information landscape*. Although increasing the kinds and specificity of signals that can be detected and processed can lead to improved decision making, it almost always comes at an increased cost. The greater the spatial and temporal complexity of the environment, the greater are the costs of incomplete information and the more advantageous is the development of improved information-gathering capabilities. Studies with simulation models suggest how variability in the spatial structure of source and signal landscapes may control patterns of animal movement that could be represented in the trace fossil record. Information landscapes and the corresponding sensory systems should have evolved in concert with major transitions in the history of life. The Ediacaran to Cambrian interval is one of the most intensively studied periods in the history of life, characterized by the profound environmental and biological changes associated with the bilaterian radiation. These include the advent of macroscopic predation, an increase in the size and energy content of organisms, and the transition in seafloors from laminated matgrounds to mixgrounds produced by the development of macroscopic infaunal bioturbation. The overall effect of these transitions was to markedly increase the spatial complexity of the marine environment. We suggest that this increased spatial complexity, in turn, drove the evolution of macroscopic sense organs in mobile bilaterians, leading to their first appearance during the Cambrian. The morphology and distribution of these sense organs should reflect the life habits of the animals that possessed them. Our overall hypothesis was that there was a “Cambrian Information Revolution,” a coevolutionary increase in the information content of the marine environment and in the ability of and necessity for organisms to obtain and process this information. A preliminary analysis of the Maotianshan Shale (Chengjiang) biota indicates that the distribution of eyes and antennae in these animals is consistent with predictions based on their life habit.

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Introduction

Peterson et al. (2008) pointed out that organisms in the Ediacaran were fundamentally confined to an essentially two-dimensional world, conscribed by biomats. In contrast, the early Cambrian world was recognizably three-dimensional, with both an incipient infauna and the first known pelagic eumetazoans (Vannier et al. 2007;

Hu et al. 2007). In this paper we will argue that this shift was accompanied by, and in fact was inextricably linked to, the evolution of macroscopic sense organs.

Paleontologists have previously reviewed the distribution and morphology of particular fossil sense organs, such as the eyes of trilobites and other early arthropods (Clarkson et al. 2006; Schoenemann 2006), or have noted the presence or absence of macroscopic

sense organs in specific Cambrian taxa (e.g., Zhang and Shu 2007). Various papers have discussed, on genetic and developmental grounds, the potential existence of sensory cells, sensilla, and organs in ancestral Metazoa and Bilateria (Knoll and Carroll 1999; Erwin 2005; Jacobs et al. 2007; Shubin et al. 2008). We are not, however, aware of any studies of the fossil record of sense organs that focus on the ecological context of their early evolution.

The broader goal of this paper is to place the evolution of sense organs of mobile organisms during the Ediacaran-Cambrian in the context of the profound environmental and biological changes occurring during this interval, such as the bilaterian radiation (Briggs and Fortey 2005; Budd 2008), the advent of macroscopic predation (Babcock 1993, 2003; Bengtson 2002; Dzik 2005; Peterson 2005), and the Cambrian substrate revolution (Bottjer et al. 2000). In particular, we will focus on the potential impact of these shifts on aspects of spatial heterogeneity relevant to the sensory ecology of mobile organisms. Evidence from a preliminary analysis of sense organs in the Maotianshan Shale biota will illustrate how ancient patterns of sense organ distribution can be interpreted in the context of life habits.

Our overarching hypothesis is that the evolution of the perceptual abilities of mobile organisms was both driven by, and a driver of, the cascading changes that characterize the Cambrian radiation. We suggest that there was a "Cambrian Information Revolution," a coevolutionary increase in the potentially available information content of the marine environment and in the ability of and necessity for organisms to obtain and process this information.

Sensory Ecology and Information Landscapes

Information and Its Costs.—In the context of this paper, we will use the often informal term "information" to refer to signals received from the external environment that could potentially lead to a response by the organism (for related formulations, see Danchin et al. 2004; Dall et al. 2005b). In this

context, a signal must be generated, transmitted, detected, processed and potentially responded to in order to become information. Following Dukas (2002), these later stages comprise "cognition"; i.e., the internal processing of the signal, from detection to possible action. Information is thus defined relative to the organism, but it is created outside of the organism; it is signals with cognition.

This concept of information is related to the idea of a "navigation capacity" in the movement ecology paradigm of Nathan et al. (2008). The navigation capacities of mobile organisms are the cognitive and sensory traits that enable them to obtain and process information about their external environment, which they then use to determine whether and where to move.

The ability to obtain, process, and act upon information about the environment is essential for the survival of any life form. As pointed out by Dall et al. (2005a), organisms are continually forced to make behavioral decisions in the face of uncertain and incomplete information. At the same time, as the external environment changes, the organism must continually obtain new information in order to reduce uncertainty and make the most advantageous decisions.

It can be assumed that there should be strong selection for features that reduce uncertainty; the more signals that can be detected and analyzed (the more information) the greater the ability to make the "right decision." These features could include developing behaviors where the organism takes time to assess its surroundings carefully, such as increased vigilance for potential predators, the evolution of more sensitive sensory structures for gathering information, or the development of sophisticated nervous systems for analyzing and acting on information.

However, as again pointed out by Dall et al. (2005a), reducing uncertainty also has a cost to the organism. In the case of increased vigilance, for example, this comes at the expense of other activities, such as mating and feeding. Similarly, building morphologic structures, producing sensory molecules, and carrying out neurological processing also

have costs associated with them. In the statistical decision framework suggested by Dall et al. (2005a), incurring these costs is acceptable only if they are exceeded by the value of improved decisions based on the information gained.

Information Landscapes.—Environments that are heterogeneous in some property over space can be described as landscapes (Turner et al. 2001; Turner 2005). For mobile animals, navigating within a landscape requires the abilities to determine the presence and location in space of entities such as resources, mates, competitors, and predators and to update this information continually as the organism moves (Dusenbury 1992; Nathan 2008).

For an animal to detect an entity in the landscape, the entity (source) must be present, there must be a signal of some kind that reaches the animal from the source, and the animal must be capable of detecting and processing the signal. We can thus view this landscape in three ways:

1. The *object* or *source landscape* describes the actual location in space of the objects of interest; these are the sources of the signals that could reach the organism.
2. The *signal landscape* is the spatial distribution of the signals; it results from the interaction of the processes of signal propagation with the pattern of signal sources.
3. The *information landscape* is the distribution of the signals as sensed by the organism; it is determined by the animal's ability to detect and process the available signals.

The landscape ecology framework allows us to characterize the spatial and temporal complexity of each of these conceptual landscapes (Turner et al. 2001). The first component of complexity is the number of kinds of entities that are present in each kind of landscape. For the source landscape, this is the number of source types; for the signal landscape, it is the variety of signals that can be traced back to each source; and for the information landscape, it is the kinds of signals that a particular organism can detect.

The second component of complexity is the spatial distribution of these entities, which



FIGURE 1. Simulated source landscape. Space is a 50×50 square lattice; 5% of the sites are occupied by at least some resource. Darker colors represent higher resource concentrations.

can also be changing over time. For each entity type considered independently, it is the nature and extent of the inhomogeneity or clumping of its distribution on the landscape, that is, the extent to which it occurs in discrete spatial patches and the geometry and distribution of these patches. For multiple entities, it is their spatial correlation, the extent to which they do or do not occur together. Note that this aspect of complexity is defined relative to the scale of the organism. What may be spatially homogeneous to a large organism (e.g., a shark swimming above a seagrass bed) may be complex to a small one (a snail living within the grass bed) and vice versa.

Figure 1 illustrates a simple source landscape with fixed and randomly distributed resource sites (Plotnick 2007). The landscape is modeled as a 50×50 square lattice, with 5% of the sites occupied by a resource. The resource concentrations at each occupied site vary randomly from 0.000 to 1.000.

Each source may emit a range of signals of widely different physical and chemical properties. Signal landscapes result from the variable transmission of these signals from each source. To a first approximation, they include far-field and near-field components. Near-field includes signal sources in direct contact with the organism, whereas far-field encompasses signals from sources located some distance away. For example, although

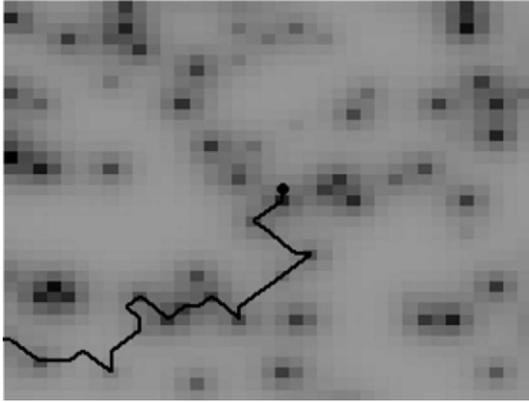


FIGURE 2. Simulated odor landscape produced by symmetrical signal dispersal from sources shown in Figure 1. Line represents movement path of an organism that follows gradients to sources and ingests them.

there are numerous sensory modalities, for virtually all marine organisms the principal source of information about their environment is through detecting chemicals (odorants) emitted by other organisms. Chemoreception can be divided into near-field or contact chemoreception in which the organism is in direct physical contact with the source of the chemicals, and far-field or distant chemoreception where chemicals (odorants) are transported through a medium to the chemosensory cells.

The odor signal landscape is the spatial distribution of odorants and is produced by the interaction of emitted odorants with fluid transport processes. This corresponds to the "odor landscape" as discussed by Atema (1996) and Moore and Crimaldi (2004). This interaction is highly scale and environment dependent, e.g., air versus water, open-flow versus interstitial (Weissburg 2000).

For small organisms, the chemical signal distribution is controlled by diffusion and is reflected in concentration gradients. This may also be the case for most mobile infaunal organisms, including larger forms, although this has been little studied (Purschke 2005; Lindsay et al. 2004).

At larger scales in open flow, chemical signals are transported by bulk flow and are characterized by turbulence-induced spatially and temporally complex odor plumes (Vickers 2000). Because these plumes are turbulent,

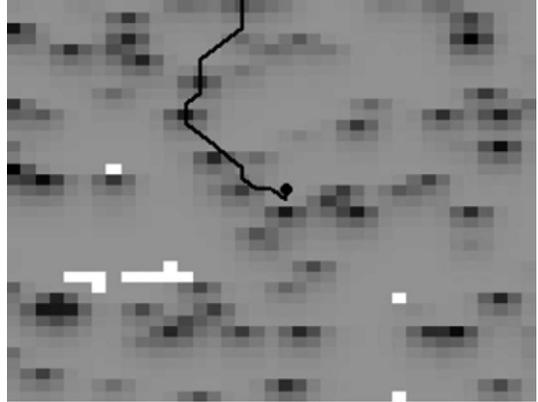


FIGURE 3. Simulated odor landscape produced by asymmetrical signal dispersal from sources shown in Figure 1. Dispersal is biased to flow from top to bottom. Line represents movement path of an organism that follows gradients to sources and ingests them. Dot is starting location.

the signal is patchily distributed and intermittent; it is often noticeably filamentous.

Figure 2 shows a model odor signal landscape resulting from dispersion from the sources in Figure 1. The signal is presumed to disperse equally in all directions and to decrease in strength exponentially from each source. The strength of the odor signal at any given location results from the mixing of signals from multiple sources. Figure 3 illustrates the odor landscape resulting from the same source landscape, but with movement constrained to flow only from top to bottom, mimicking the effect of flow. Notice that the odor signal landscape is more homogeneous than the corresponding source landscapes. Although the sources are spatially isolated, the resulting signal landscapes are connected.

Information landscapes result from the interaction of the signal with receptors and from its interpretation by the nervous system. These have both biological and physical components and are again strongly influenced by scale and habitat. First, organisms differ widely in the types of signals and minimum signal strength they can detect (Ache and Young 2005). Humans, for example, have lost the ability to detect numerous odorants, but have acquired color vision.

Chemoreception is clearly scale dependent. Minute organisms, including small metazoans, generally move in response to changes in

signal strength associated with moving up or down a chemical gradient (Vickers 2000; Weissburg 2000). They usually detect this gradient by sampling sequentially as they move. Larger organisms, in contrast, must navigate in response to turbulent odor plumes. The presence of directional flows imposes structure on the signal landscape that strongly affects the ability of an organism to detect the sources of a signal. Because the odor source must be upstream of the animal, when an animal detects a plume it turns to move upstream (rheotaxis). Once in the odor plume, these organisms use zigzag movements and/or bilateral sense organs to maintain themselves within the plume (Weissburg 2000).

Scaling and habitat issues also apply to photoreception. Simplistically, photoreception can be grouped into three main functional levels (Cronin 1986; Land and Nilsson 2002, 2006; Schoenemann 2006). The first of these is simply the detection of light intensity, which allows the recognition of the direction of light. This can be accomplished by a single photoreceptor. Detection of movement occurs when multiple photoreceptors are sequentially darkened. Land and Nilsson (2006) classify these as "eyes" because they detect spatial information. The formation of images requires the most complex visual and neurologic equipment. Non-image-forming eyes, such as those on the mantle margin of scallops, which only detect movement, pass on far less visual information for processing than the multi-purpose eyes of organisms such as cephalopods (Land and Nilsson 2006).

The various senses of larger mobile organisms often do not act independently; instead, navigation often requires the use of multiple sensory modalities. In order to apply rheotaxis, an animal must be able to determine flow direction relative to its current position. As discussed by Vickers (2000), animals living on the substrate can use mechanoreceptors to detect flow direction. Flying and free-swimming organisms, however, must use vision to find their location relative to fixed reference points, in order to distinguish relative (a combination of flow and its own locomotion) from absolute fluid movement. An analogy

would be air speed versus ground speed in an airplane; the latter cannot be determined without an outside reference. Experiments with *Drosophila* (Frye et al. 2003, Gilbert and Kuenen 2008) and moths (Goyret et al. 2007) show that they require visual cues in order to navigate effectively in an odor plume. Similarly, sharks in which the lateral line has been experimentally disabled rely on visual cues to determine flow direction (Gardiner and Atema 2007).

Figures 2 and 3 show simulated movement patterns of an organism possessing both contact and distant chemoreception. It moves in the direction of strongest detected signal and ingests the sources when it reaches them (for model details, see Plotnick 2007; Koy and Plotnick 2007). Note that the organism moves not in response to the distribution of the sources, but to the strength and distribution of the signals. In the case of directional flow, it may miss a rich source that is close by because it is "downstream."

Information Costs and Landscape Complexity.—There should be a correlation between the spatial and/or temporal heterogeneity of a mobile organism's environment and its ability to obtain and process information. The simplest situation would be an organism feeding on a single resource type that is continuously distributed. As shown by Plotnick (2007), efficient foraging in this setting requires only contact chemoreception and the ability to distinguish stronger from weaker signals. Such an organism does not require more sophisticated sensory or neural abilities; they would be an unnecessary cost.

A more complicated situation would be one where the signal sources are spatially separated. In this case, efficient foraging requires detection of signals coming from sources that are not in direct contact with the organism (Plotnick 2007) and a concomitant increase in the sophistication of sensory organs and neural processing; e.g., it is necessary to determine source direction and possibly distance.

Finally, many organisms do not feed on a single resource and are themselves potentially subject to predation, possibly from multiple predators. They also need to locate mates.

These animals need to be able to detect and interpret signals from all of these sources. The cost of not being able to do so would be high.

Therefore, whereas in relatively simple and relatively homogeneous settings, the advantage to developing sophisticated sensory abilities is exceeded by the cost, in heterogeneous and patchy settings there is a significant cost to incomplete knowledge. The more complex the source and signal landscapes are, the greater the cost of incomplete information about that complexity. Investment in improved sensory and neural capabilities therefore becomes worthwhile.

Ediacaran–Cambrian Landscapes

In this section we will argue that the spatial heterogeneity of the marine environment of mobile organisms increased markedly during the Cambrian relative to the Ediacaran. This increase in landscape heterogeneity occurred both in the number of signal source types that these animals needed to be cognitive of and in the spatial heterogeneity of the distribution of these sources, involving both benthic and pelagic environments. At the same, an increase in the maximum size of mobile organisms, as well as the advent of nektonic forms, changed the relevant physical environment of signal propagation and detection.

Cambrian Diversity and Disparity Radiation.—Despite some skepticism (Levinton 2008), molecular clock and paleontological evidence are increasingly seen as in agreement in placing the initial bilaterian radiation as occurring during the later part of the Ediacaran (Peterson et al. 2008). The empirical fossil record, of course, still supports a major increase in diversity and disparity at all taxonomic levels throughout the Cambrian and at lower taxonomic levels into the Ordovician (Briggs and Fortey 2005; Droser and Finnegan 2003; Marshall 2006).

It can be assumed that the increase in diversity of forms, each of which could represent potential predator, prey, or competitor, would have been accompanied by an increase in the number of available signals in the environment. This would have greatly increased selection pressure for mechanisms for identifying and discriminating among these signals.

Cambrian Substrate Revolution.—The increase in bioturbation depth and intensity through the Cambrian has been documented in a broad spectrum of siliciclastic and carbonate marine environments throughout the globe, and it led to a critical change in dominant seafloor substrates (Seilacher and Pflüger 1994; Bottjer et al. 2000). In strong contrast to modern marine settings, the late Proterozoic was characterized by seafloor environments dominated by microbial mats, which led to the formation of ubiquitous microbial textures, stromatolites, and thrombolites in carbonate settings (Riding and Awramik 2000) and a variety of microbially mediated sedimentary structures in siliciclastic settings (Hagadorn and Bottjer 1997, 1999; Schieber 1999). It has been hypothesized that the Ediacaran biota had lifestyles adapted to survival on such microbial-mat-bound substrates (Seilacher and Pflüger 1994; Seilacher 1999).

The Cambrian is marked by the onset and intensification of vertical bioturbation. This was probably due to a coevolutionary process of organisms escaping benthic predators and benthic predators following prey into the substrate (Bengtson 2002; Babcock 2003; Dzik 2005). The result was a fundamental shift in dominant substrate types in normal marine settings. This transition was from typical Proterozoic-style soft substrates with a low water content, a sharp sediment-water interface, and well-developed microbial mats, to typical Phanerozoic-style soft substrates with a well-developed mixed layer, a higher water content, and an easily resuspended, diffuse sediment-water interface (e.g., Droser and Bottjer 1988; Droser et al. 1999, 2002; Hagadorn and Bottjer 1999; Seilacher 1999; Seilacher and Pflüger 1994).

In addition, abundant, well-developed seafloor microbial mats were relegated to stressed settings with inhibited metazoan activity (e.g., Hagadorn and Bottjer 1997, 1999). The effect of this change in dominant substrate types on the ecology and evolution of non-burrowing benthic metazoans has been termed the “Cambrian substrate revolution” by Bottjer et al. (2000).

The Cambrian substrate revolution resulted in an increasingly heterogeneous seafloor environment during much of the Cambrian,

as bioturbation levels climbed to typical Phanerozoic levels. Some settings had substrate conditions analogous to Precambrian substrate conditions, complete with microbial mats, whereas others showed signs of advanced mixed-layer development. The end result was a much patchier landscape for animals to interact with, especially when compared with the more homogeneous seafloor conditions of the Ediacaran.

Evolution of the Plankton and Nekton.—Simultaneous with the modification of the benthos, several studies have convincingly argued that the evolution of the pelagic realm was a key part of the Cambrian explosion. Signor and Vermeij (1994) suggested that the diversification of metazoan members of the plankton, in particular long-lived feeding larvae, did not occur until the late Cambrian and suggested that this was a response to increased benthic predation and bioturbation. This interpretation is generally supported (Peterson 2005) by molecular clock estimates of the origins of lecithotrophic and non-lecithotrophic larvae, with non-feeding larvae being short-lived members of the plankton during the early Cambrian, and feeding larvae arising multiple times in the late Cambrian–Middle Ordovician.

Butterfield (1997) suggested that planktotrophy emerged during the early Cambrian with the development of the mesozooplankton (small herbivorous metazoans). Vannier et al. (2007) identified the presence of chaetognaths, a major pelagic predator on small crustaceans, in the lower Cambrian Chengjiang biota. They also supported the identification of protoconodonts, which occur in the earliest Cambrian, as grasping spines of chaetognaths. This suggests the presence of their mesozooplankton prey, and thus of at least three-tier food webs, by quite early in the Cambrian (Vannier et al. 2007). Mechanisms for resource/prey detection and predator avoidance must have accompanied this development.

Origin of Macroscopic Predators.—The earliest direct evidence for predation is the borings on the Ediacaran form *Cloudina* (Bengtson and Zhao 1992; Hua et al. 2003). Bengtson and Zhao (1992) measured boring

diameters of 40–400 μm on tubes, whereas Hua et al. (2003) found 20–85 μm diameter holes on tubes 200–400 μm in diameter. After comparing these with modern naticid borings, Bengtson and Zhao suggested that the unknown predator was no larger than *Cloudina* itself, and thus in the range of modern meiofauna (<500 μm). If so, it can be assumed that this predator used chemical gradients to locate its sessile benthic prey.

Larger benthic and pelagic predators are certainly well developed by the time of the Chengjiang biota (Vannier and Chen 2000; Brett and Walker 2002; Bengtson 2002; Dzik 2005; Peterson et al. 2005). As noted above, eyes would be a necessary complement to chemoreception in mobile nektonic forms. Presumed Cambrian predators, such as anomalocaridids and various euarthropods including trilobites, were equipped with well-developed eyes (Parker 1998; Babcock 2003; Schoenemann 2006) and many possessed antennae (see below).

The advent of large and active predators also should have led to a response by their prey. Bengtson (2002), Babcock (2003), and Dzik (2005) identified the development of skeletons and infaunalization as responses to increased predation. We would add to this the elaboration of sensory and nervous systems for recognizing and responding to potential predators, a point clearly made by Babcock (2003) in terms of trilobites. Fernald (2004) pointed out the coincidence of eye evolution with predation, but suggested it was only one of multiple selective forces operating.

We thus propose a scenario (following Peterson 2005) in which benthic predation, which requires chemoreception and probably mechanoreception, but not sophisticated eyes, evolved first. The advent of the pelagic realm then produced small predators, such as chaetognaths, that rely on mechanoreception. These were followed by macroscopic nektonic predators, which required sophisticated visual systems. These, in turn, led to increased visual sensory abilities by prey organisms, including predominantly benthic organisms such as trilobites (which were probably also predators [Babcock 2003]).

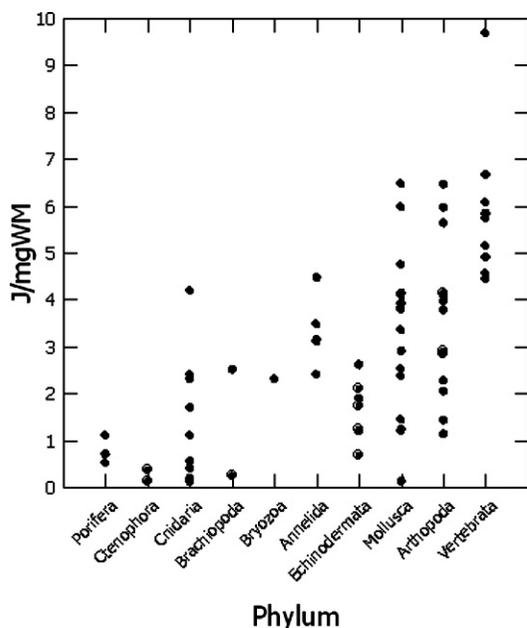


FIGURE 4. Energy content of soft tissues of marine phyla, in units of joules per milligram wet mass (J/mgWM). Each point represents the median value for orders within each phylum. Data from tables in Brey (2001).

Concentration of Biomass.—Predation has distinct costs involved in the location, tracking, capture, and processing of resources (Dusenbury 1992). It is thus worthwhile only if the prey item yields a net energy gain. Although the affinities of the Ediacaran biota remain a persistent problem, there remains little evidence, with the possible exception of *Kimberella* (Fedonkin et al. 2007), that it included either large mobile organisms or predators upon them. One possibility is that the Ediacaran organisms contained too little nutritive value to make predation worthwhile (Hua et al. 2003), although it is also possible that predation left no observable traces (Kowalewski 2002; Babcock 2003).

A rough estimate of the energy content of marine organisms can be obtained from the data tables published online by Brey (2001). These tables summarize available data on composition for 2300 species of marine protists, plants, and animals, including ratios of dry mass to wet mass, wet mass to shell mass, and carbon to phosphorus. These data are summarized taxonomically by phylum, class, order, and family. In Figure 4 we have plotted the median values for energy content

per unit wet mass (shell removed), in units of joules per milligram wet mass (J/mgWM), for orders within phyla common in the fossil record. It should be noted that sample sizes vary widely among taxa, with far more data available on arthropods (nearly all crustaceans), for example, than sponges (see Brey 2001 for details).

If we assume that the typical Ediacaran organism was similar in composition to cnidarians or ctenophores, their energy content was on the order of 0.2–1.6 J/mgWM. The only coelenterates with high energy content are the burrowing anemones (Ceriantharia). The average energy content of crustaceans and molluscs, in contrast, is on the order 3.5–4.0 J/mgWM and that of vertebrates even higher. Although it is uncertain whether total marine biomass increased during the Cambrian, the sequestering of more biomass in discrete and larger organisms would have made the costs of predatory behavior and related sensory abilities worthwhile. It should also be noted that the data from Brey (2001) may allow a more quantitative approach to Bambach's (1993) analysis of "seafood through time."

Size and Life Position.—The trace fossil record clearly indicates that mobile organisms in the Cambrian were much larger than those in the Ediacaran (Jensen et al. 2005). Many of the Ediacaran trace fossils may not even represent bilaterians (Pawłowski and Gooday 2009). An increase in body size, as well as a shift from grazing under biomats (undermat mining) to foraging over the substrate, would have changed the relevant fluid mechanical environment from one dominated by diffusion to one dominated by convection and thus promoted the evolution of macroscopic bilateral chemosensory organs. Similarly, vision, which would not have been relevant to undermat miners, would have become increasingly important in a shift to epifaunal and eventually nektonic modes of life (Schoenemann 2006).

Summary.—Multiple lines of evidence thus point to a major increase in spatial complexity during the Cambrian. These include two important developments:

1. Increase in the variety of producers of biologically relevant signals, resulting

from the overall increase in diversity and disparity and the advent of both benthic and nektonic predators;

2. Increase in patchiness of resource distribution, stemming from the increase in bioturbation and the sequestering of biomass into spatially discrete packages, including larger living organisms, their dead remains, and their feces.

At the same time, there were major shifts in life habit and size of mobile bilaterians organisms, in particular the advent of large mobile benthic and nektonic animals. These organisms would have been in a physical environment where the ability to detect and respond to odor plumes and complex visual signals would have been vital.

Evidence for Ediacaran-Cambrian Sensory Evolution

Early Record of Sense Organs.—As pointed out by Marshall (2006), one noticeable characteristic of the Ediacaran biota is the lack of any discernible macroscopic sense organs. This does not, however, mean that sensory abilities in animals were lacking prior to the Cambrian. The ability to sense and react to external stimuli almost certainly arose simultaneously with life itself.

The presence of simple trace fossils, including probable feeding traces of *Kimberella* (Fedonkin et al. 2007) and the borings on *Cloudina*, hints that at least contact chemoreception was present in early bilaterians (Plotnick 2007). In addition, compelling phylogenetic evidence points to the early evolution of animal sensory systems (Jacobs et al. 2007). For example, the presence of opsins in hydrozoans, but not in sponges, fungi, or parazoans (Plachetzki et al. 2007), suggests that phototransduction cascades based on these visual pigment proteins are a shared feature of Eumetazoa. It is likely, therefore, that Ediacaran bilaterians were photosensitive.

Little information regarding sensory organs is found in the small shelly fossil records of the lowest Cambrian stages (Fortunian and Stage 2). (Note: Cambrian stage names used herein are those currently suggested by the

International Commission on Stratigraphy [Babcock et al. 2005; Landing et al. 2007].) If protoconodonts indeed represent the remains of chaetognaths (Vannier et al. 2007), then at least some bilaterians at this time had the ability to detect light direction. Chaetognaths predominantly use mechanoreception for prey detection; their lenses lack the ability to form images and primarily function in diel movements (Feigenbaum and Maris 1984).

Phylogenetic studies have identified the presence of lateral and compound eyes and of simple median eyes as a primitive characteristic of arthropods (Wills et al. 1998; Waloszek et al. 2007; Ma et al. 2009). The earliest preserved visual systems are the holochroal eyes of the earliest trilobites at the base of the Cambrian Stage 3 (Clarkson et al. 2006). We can safely assume that these trilobites also possessed antennae, given that they are preserved in trilobites of the slightly younger Chengjiang biota (Chen and Zhou 1997; Chen 2004; Hou et al. 2004).

The Chengjiang biota provides the earliest evidence of the widespread development of sensory organs. Large eyes occur in numerous arthropod taxa, such as *Isoxys* (Vannier et al. 2009). The stem arthropod *Fuxianhuia* apparently possessed large stalked compound eyes (Budd 2008) and short antennae. The antennae lack any indication of setae. Large compound eyes are, of course, a distinctive feature of the stem arthropods *Anomalocaris* and the Burgess Shale *Opabinia*. Dorsal median eyes and stalked ventral eyes have been identified in *Leanchoilia* (Schoenemann 2006).

Within the lobopodians, *Hallucigenia* might have had a simple type of visual system, such as eyespots (Ma et al. 2009). Ma et al. (2009) identified paired lateral simple eyespots, as well as antenna-like anterior head structures, in the Chengjiang lobopod *Luolishania longicruris*. There are also numerous setae, which are suggested to have a mechanosensory function. Schoenemann (2006) identified paired simple eyes in *Luolishania*. Dzik (2003) suggested, on the basis of fossils from the early Cambrian of Kazakhstan, that the sclerites of *Microdictyon* may have been compound eyes.

The Maotianshan Shale biota shows that sensory organs had developed across a wide spectrum of phyla by that time. Panarthropods (arthropods + tardigrades + onychophora) dominated epifaunal and planktonic realms, but image-forming eyes and antennae appear only in arthropods. The evolution of the head sensorial organs during the transition from the wormlike ancestral tardipolypods or lobopodians (soft-cuticled stem arthropods) through proarthropods to euarthropods (Waloszek et al. 2007) might have been triggered by an increasingly active lifestyle (Chen et al. 2007; Chen 2009).

Tardipolypods, such as *Hallucigenia*, might have had a simple type of visual system, such as eyespots, but lacked image-forming eyes (Chen and Zhou 1997). Compound eyes first appeared in proarthropods such as *Fuxianhuia* and *Shankouia*. The primitive condition of the image-forming eyes in arthropods was stalked, giving these animals a wide field of vision. Proarthropods were not predators, suggesting that the development of image-forming eyes in these arthropods was not triggered by visual hunting but likely by visual feeding and escaping (Chen 2009).

The long and multisegmented flagelliform antennae that occurred widely among euarthropods, including trilobites, probably functioned as both a chemoreceptor and tactile receptor. They are missing in all the tardipolypods and first appeared in proarthropods. The primitive condition of the antennae, as exemplified by the proarthropods *Fuxianhuia* and *Shankouia*, was short and limb-like, probably lacking in sensorial setae.

Image-forming paired eyes are an evolutionary novelty of the Crustozoa (including all known craniates and their immediate precraniate precursors [Mallatt and Chen 2003; Chen 2008]). The paired eyes in the earliest crustozoans, as exemplified by the early Cambrian *Haikouella*, *Yunanozoon*, and *Hai-kouichthus*, are relatively round and large, ranging from 0.2 to 0.6 mm in diameter. They might have resembled those in extant vertebrates, having many neurons that are packed in layers and are able to form an image. In contrast, amphioxus has four much smaller photoreceptors (Lacalli 2004), none of which

are capable of forming images. As in the arthropods, the evolution of the image-forming eyes in Crustozoa might have been triggered by an increasingly active lifestyle (Chen 2009).

Arthropods with eyes and antennae dominated the epifaunal and planktonic realms, whereas priapulid worms with sensory setae dominated infaunal settings (e.g., Chen and Zhou 1997; Dornbos and Chen 2008; Chen et al. 2007; Maas et al. 2007). The same features are seen in the middle Cambrian Burgess Shale biota (e.g., Caron and Jackson 2008).

Eyes and Antennae in the Chengjiang Biota

We are currently conducting a study of the quantitative distribution of sense organs in the Cambrian and their relationship to habitat and life mode. The initial phases of this study have focused on the distribution of eyes and antennae within mobile organisms of the Chengjiang biota.

The Stage 3 Cambrian (= Qiongzhusian, = Atdabanian) Maotianshan Shale (Chengjiang) biota of southwest China contains a minimum of three discrete fossil assemblages, known as the Shankou biota, Haikou biota, and Chengjiang biota proper. Collections of these three assemblages, totaling over 40,000 specimens, are stored at the Early Life Research Center (ELRC) in Chengjiang, and the Nanjing Institute of Geology and Palaeontology, Academia Sinica (NIGPAS) in Nanjing. These assemblages were collected from three different localities, and at each locality every attempt was made to not discard specimens during collection. The ELRC and NIGPAS collections, therefore, consist of three distinct, thoroughly sampled assemblages, each of which represents a time-averaged community.

Our pilot study has examined sense organs in taxa from the Shankou biota. For each taxon, its relative abundance and the presence/absence of macroscopic sensory organs has been recorded. To ensure that the counts provide a census of animals that were actually alive on the seafloor, we counted only specimens interpreted as buried alive, on the basis of either undecayed soft-part preservation or fully articulated complex skeletons. Abundance data were collected at the

genus level. These genera are almost universally monospecific, but focusing this study at the generic level mitigates any potential problems caused by taxonomic oversplitting at the species level. The life habits and feeding modes of each genus were estimated as accurately as possible from previously published interpretations (Appendix 1). In order to avoid circular reasoning, we examined these previous life mode interpretations to ensure that sensory organ presence/absence was not a principal part of their rationale. The categories utilized in this study are comparable to those of Conway Morris (1986), Caron and Jackson (2008), and Dornbos and Chen (2008): Infaunal sessile (IS), Infaunal vagrant (IV), Epifaunal sessile (ES), Epifaunal vagrant (EV), Nektobenthic (NK), Pelagic (PE), and Unknown (UN). The feeding type categories are Suspension (SU), Deposit feeder (DE), Hunter/scavengers (HS), and Unknown (UN).

A total of 21,869 specimens were tallied from the Shankou biota. Mobile epifaunal and nektonic genera, which comprised 31 genera and 7 life modes, constituted 5597 of these specimens. Presence/absence data of macroscopic sensory organs (eyes and antennae) were collected from these 31 genera, and these data were mapped onto the relative abundance and life mode data. Arthropods dominate this data set, constituting 21 of the 31 genera and 93.7% (5,247) of the specimens examined (Appendix 1).

The results reveal an interesting difference in the sensory organ distribution between mobile epifaunal and nektonic forms. Whereas the presence of antennae is ubiquitous in both mobile epifaunal and nektonic genera (97.8% of mobile epifaunal and 94.2% of nektonic specimens have antennae), only nektonic genera are overwhelmingly dominated by forms with eyes (94.5% of specimens). In contrast, only 62.8% of mobile epifaunal specimens possess eyes (Table 1). As outlined above, this significant difference in eye presence may lie in the importance of vision for determining flow direction for nektonic forms.

Our preliminary results suggest two general hypotheses: (1) that essentially modern

TABLE 1. Percentage of specimens with eyes and antennae in the Shankou biota, related to life habit.

Life habit	Total	% Eyes	% Antennae
Epifaunal	4283	62.8	97.8
Nektonic	1235	94.5	94.2

sensory systems evolved early in metazoan evolution; and (2) that sensory systems should differ between benthic and nektonic forms. Even by early in the Cambrian, there does appear to be a difference in the selective pressure to develop certain sensory organs based on the local environment of an organism and its life mode. We predict that further data collection will strengthen the evidence for this pattern and provide evidence for similar patterns later in the Cambrian and Paleozoic.

Conclusions: The Cambrian Information Revolution

Our central hypothesis is that the development of complex sensory systems and by implication sophisticated nervous systems (Holland 2003) occurred as a consequence of the Cambrian radiation of mobile bilaterian taxa and a concomitant increase in the spatial complexity of the marine environment. In particular, we are suggesting that both source and signal information landscapes evolved rapidly during from the Ediacaran into the Cambrian, becoming more heterogeneous and patchy. This change resulted from a combination of the Cambrian substrate revolution, which disrupted previously existing microbial mat substrates, the origin of active macroscopic predators, and the sequestering of organic matter in larger and more biomass-rich organisms. The increased complexity of the information landscapes increased the cost of incomplete information and thus promoted improvements in morphological and neurobiological abilities to obtain and process information. In addition, larger mobile bilaterians of the Cambrian, in particular epibenthic and nektonic forms, would have lived in a fluid regime that selected for the development of macroscopic bilateral sense organs.

We thus view the evolution of macroscopic sense organs as part of the cascade of

ecological and evolutionary feedbacks occurring during this interval (Marshall 2006; Budd 2008). In this scenario, sophisticated sense organs would not have developed at the onset of the interval, but would have developed concomitantly with other changes associated with the Cambrian radiation. This is compatible with the first appearance of complex sense organs, such as the eyes of trilobites, some 20 Myr after the beginning of the Cambrian.

This hypothesis differs markedly from the "light-switch" theory proposed by Parker (1998, 2003), which stemmed from his observation that the surface texture of various Burgess Shale organisms, e.g., *Wiwaxia* and *Marella*, would have made parts of them iridescent. Interpreting this as a tactic to avoid visual predators, Parker suggested that it was the evolution of eyes, in particular image-forming eyes for predation, that triggered the Cambrian explosion. As Parker put it (2003: p. 291): "So that evolution of vision by that very first eye in a trilobite triggered the Cambrian explosion."

Conway Morris (2003) and Erwin (2003), in their reviews of Parker (2003), pointed out the most glaring problem: the earliest trilobites appeared long after the Cambrian explosion was well under way, at the beginning of Stage 3. We would also point out here that eyes are not necessary for predation. Among mobile benthos, asteroids are voracious predators that rely exclusively on chemoreception for prey detection, although they are light sensitive (Beddingfield and McClintock 1993; Brewer and Konar 2005). Similarly, most gastropods rely on chemoreception and have eyes that do not allow motion detection (Land and Nilsson 2006). As discussed earlier, one of the most important groups of small pelagic predators is the chaetognaths, which apparently use mechanoreception rather than vision for prey detection. In sum, although we agree with Parker concerning the importance of the evolution of vision during the Cambrian, we feel that the central tenets of his hypothesis are flawed. We would certainly reconsider if complex eyes are discovered in forms from the earliest Cambrian or latest Ediacaran.

The evolution of sense organs is part of a wider picture of the development of neurological systems (Holland 2003) and behavior during the Cambrian radiation. Detailed examination of sensory organ distribution and morphology in Cambrian arthropods, as well as other phyla, should elucidate much more about the evolution of sensory organs in early animals and its contribution to the ecological feedbacks that fueled the Cambrian radiation. Understanding the history of the interactions between the changing landscape of spatial signals and the ability of organisms to detect and react to this variability should give new insights into both the body and trace fossil record during this interval.

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Appendix 1

Occurrence of eyes and antennae in genera from the Shankou biota. Counts are actual number of specimens. Total count = 5597. For ecology, first two letters are life habits and second two are feeding types. Life habits: Infaunal sessile (IS), Infaunal vagrant (IV), Epifaunal sessile (ES), Epifaunal vagrant (EV), Nektobenthic (NK), Pelagic (PE), and Unknown (UN). The feeding type categories are Suspension (SU), Deposit feeder (DE), Hunter/scavengers (HS), and Unknown (UN). Morphology based on information in Butterfield (2002), Caron, (2005), Chen and Huang (2004), Chen et al. (2005), Chen and Zhou (1997), Fortey and Owens (1999), Hou et al. (1999, 2004), Hu (2005), Ramsköld and Edgecombe (1996), Shu et al. (1999), Shu and Zhang (1996), and Vannier and Chen (2000, 2002, 2005).

Genus	Taxon	Count	%	Ecology	Eyes	Antennae
<i>Leanchoilia</i>	Euarthropoda	2143	38.3	EVHS	Yes	Yes
<i>Naraoia</i>	Euarthropoda	696	12.4	EVHS	No	Yes
<i>Primicaris</i>	Euarthropoda	642	11.5	EVSU	No	Yes
<i>Isoxys</i>	Euarthropoda	593	10.6	NKHS	Yes	Yes
<i>Waptia</i>	Euarthropoda	570	10.2	NKDE	Yes	Yes
<i>Eoredlichia</i>	Euarthropoda	208	3.7	EVHS	Yes	Yes
<i>Kunmingella</i>	Euarthropoda	112	2.0	EVHS	Yes	Yes
<i>Microdictyon</i>	Lobopodia	107	1.9	EVHS	No	Yes
<i>Ambrolinevitus</i>	Hyalolithida	80	1.4	EVDE	No	No
<i>Xandarella</i>	Euarthropoda	68	1.2	EVHS	Yes	Yes
<i>Vetulicola</i>	Unknown	68	1.2	NKSU	No	No
<i>Branchiocaris</i>	Euarthropoda	68	1.2	NKHS	?	?
<i>Cardiodictyon</i>	Lobopodia	65	1.2	EVHS	No	Yes
<i>Yunnanocephalus</i>	Euarthropoda	46	0.8	EVHS	Yes	Yes
<i>Shankouia</i>	Euarthropoda	28	0.5	EVHS	Yes	Yes
<i>Fuxianhuia</i>	Euarthropoda	28	0.5	EVHS	Yes	Yes
<i>Vetustovermis</i>	Mollusca (?)	21	0.4	EVDE	Yes	Yes
<i>Cindarella</i>	Euarthropoda	14	0.3	EVHS	Yes	Yes
<i>Fortiforceps</i>	Euarthropoda	7	0.1	EVHS	Yes	No
<i>Acanthomeridion</i>	Euarthropoda	6	0.1	EVUN	?	?
<i>Retifacies</i>	Euarthropoda	5	0.1	EVHS	Yes	Yes
<i>Amplectobelua</i>	Anomalocaridid	3	0.1	NKHS	Yes	No
<i>Kuamaia</i>	Euarthropoda	3	0.1	EVHS	Yes	Yes
<i>Parapaleomerus</i>	Euarthropoda	3	0.1	EVUN	?	?
<i>Saperion</i>	Euarthropoda	3	0.1	EVHS	Yes	Yes
<i>Paucipodia</i>	Lobopodia	2	0.04	EVHS	No	No
<i>Urokodia</i>	Euarthropoda	2	0.04	EVUN	?	?
<i>Jiangfengia</i>	Euarthropoda	2	0.04	EVHS	Yes	No
<i>Banffia</i>	Unknown	2	0.04	EVDE	No	No
<i>Anomalocarisis</i>	Anomalocaridid	1	0.02	NKHS	Yes	No
<i>Hallucigenia</i>	Lobopodia	1	0.02	EVHS	No	Yes