




Article

# The Phanerozoic aftermath of the Cambrian information revolution: sensory and cognitive complexity in marine faunas

Shannon Hsieh\* , Roy E. Plotnick , and Andrew M. Bush 

**Abstract.**—The Cambrian information revolution describes how biotically driven increases in signals, sensory abilities, behavioral interactions, and landscape spatial complexity drove a rapid increase in animal cognition concurrent with the Cambrian radiation. Here, we compare cognitive complexity in Cambrian and post-Cambrian marine ecosystems, documenting changes in animal cognition after the initial Cambrian increase. In a comparison of Cambrian and post-Cambrian Lagerstätten, we find no strong trend in the proportion of genera possessing two types of macroscopic sense organs (eyes and chemoreceptive organs such as antennae, feelers, or nostrils). There is also no trend in general nervous system complexity. These results suggest that sophisticated information processing was already common in early Phanerozoic ecosystems, comparable with behavioral evidence from the trace fossil record. Most taxa capable of complex information processing in Cambrian ecosystems were panarthropods, whereas mollusks and chordates made up larger proportions afterward. In both the Cambrian and the present day, ecological occupation of diverse habitat tiers and feeding modes is possible with even simple nervous systems, but ecological lifestyles requiring rapid, regular movement are almost exclusively associated within brain-bearing taxa, suggesting a connection with fast information-processing abilities and bodily responses. The overall rise in cognitive sophistication in the Cambrian was likely a unique event in the history of life, although some lineages subsequently developed more elaborate sensory systems and/or larger brains.

Shannon Hsieh† and Roy E. Plotnick. Department of Earth and Environmental Sciences, University of Illinois at Chicago, 845 West Taylor Street, Chicago, Illinois 60607, U.S.A. E-mail: [shsieh7@uic.edu](mailto:shsieh7@uic.edu), [plotnick@uic.edu](mailto:plotnick@uic.edu).

†Present address: Institute of Geological Sciences, Jagiellonian University, Gronostajowa 3a, 30-387 Kraków, Poland.

Andrew M. Bush. Department of Geosciences and Department of Ecology and Evolutionary Biology, University of Connecticut, 354 Mansfield Road, Storrs, Connecticut 06269-1045, U.S.A. E-mail: [andrew.bush@uconn.edu](mailto:andrew.bush@uconn.edu)

Accepted: 8 December 2021

\*Corresponding author.

## Introduction

Cognition is the ability to acquire, process, and respond to information. The way animals interact with physical and biotic environments is heavily mediated through use of information, such that innovations and changes in their cognitive abilities can greatly influence their overall ecology and evolution (Dukas and Ratcliffe 2009). The origins and evolution of cognition are of intense interest to biologists, but they have been rarely examined in the fossil record.

The Cambrian radiation of metazoan animals is a critical event for understanding the origins of cognition. In the Cambrian, the world became much more complicated to navigate as the overall size, diversity, disparity, and

variety of lifestyles of macroscopic animals increased (Valentine 2002; Marshall 2006; Dunne et al. 2008; Bush et al. 2011). The spatial landscape was also transformed during the Ediacaran and Cambrian; large concentrations of biomass and organic matter produced heterogeneity (the “savannah hypothesis”; Budd and Jensen 2015) and seafloor sediments were increasingly modified by bioturbators, disrupting the stable matground surfaces that existed before (the agronomic and substrate revolutions; Seilacher and Pflüger 1994; Bottjer et al. 2000). There were benefits to being able to collect, process, and respond to information in this new, spatially and biotically complex world, such as acquiring difficult to locate resources. There were also costs borne from

missing out on information, including risks of undetected danger. Therefore, selection pressures existed for increased abilities to handle and utilize information—in other words, cognition—among mobile Cambrian bilaterian metazoans. This idea was proposed by Plotnick et al. (2010) as the Cambrian information revolution.

Though the cognition of animals is not directly preserved in their fossils, morphology and other correlates provide clues about how animals handled information. We can break down cognition into three parts—collecting, processing, and responding to information. First, an animal's ability to collect information from its surroundings can be determined from its sensory systems, reflected in the presence, or degree of development, of sense organs. Second, an animal's ability to process information can be constrained from its nervous system, remains of which have been found, albeit rarely, in well-preserved fossils. Third, how an animal potentially responded to information is revealed by its behavior, which is inferable from functional morphologic analysis and from trace fossils, the preserved results of behavior. These aspects may also be inferred phylogenetically from modern living relatives of the animal. Together, these lines of evidence allow us to reconstruct cognition and cognitive abilities in deep time.

From the sensory side, Plotnick et al. (2010) and Zhao et al. (2013) examined the Cambrian information revolution by tabulating the number and proportion of animals with macroscopic sense organs (eyes and antennae) in the Chengjiang biota, finding that they disproportionately belonged to active, mobile animals. Hunting or scavenging animals, as well as epifaunal, pelagic, and especially nektonic organisms, were most likely to have eyes. Examples of this trend are seen with the large and well-developed eyes of the swimming arthropods *Isoxys*, *Tuzoia*, and *Waptia* (García-Bellido et al. 2009; Strausfeld 2011, 2016; Vannier et al. 2018). Parker (1998, 2003) proposed that the development of eyes and vision triggered the Cambrian radiation, generating a diversity of body plans from arms races between competing organisms that could see one another, though Plotnick et al. (2010) consider that complex eyes evolved too late for this. Nonetheless,

the senses involved in the information revolution, including vision, chemoreception, and mechanoreception, likely promoted increased biotic interactions, evolution, and diversification in the Cambrian and later times.

Evidence of sophisticated information collection and processing comes from multiple studies of exquisite preservation in Cambrian fossils of complex eyes, other sensory organs, nervous systems, and brains (e.g., Chen et al. 1999; Shu et al. 2003; Paterson et al. 2011; Ma et al. 2012; Schoenemann and Clarkson 2013, 2017; Tanaka et al. 2013; Cong et al. 2014; Strausfeld 2015). Panarthropods (arthropods and their relatives), possessing a diversity of eyes and antennae and with brains resembling those of their modern counterparts (Ma et al. 2012; Tanaka et al. 2013; Cong et al. 2014; Strausfeld 2015), were particularly dominant among the active and visually oriented fauna during this period (Zhao et al. 2013). Other phyla known to be neurologically and sensorially complex today were also well represented at this time. Cambrian annelids bearing organs such as antennae and paired sensory palps included *Kootenayscolex* (Nanglu and Caron 2018) as well as *Canadia*, which was also found with an exceptionally well-preserved nervous system, suggesting that the ancestor of annelids was already reasonably cephalized (Parry and Caron 2019). The enigmatic nectocaridids, interpreted as nektonic cephalopod-like mollusks, possessed large, camera-type eyes and flexible tentacles (Smith 2013). Sensory evidence in Cambrian chordates ranges from paired tentacles in the weakly cephalized *Pikaia* (Morris and Caron 2012) to more fish-like traits in animals interpreted as craniate or vertebrate, such as the eyes, possible nasal sacs, and potential otic capsules seen in *Haikouichthys* (Shu et al. 2003). Likewise, the chordate *Haikouella* was found with a sizable preserved brain that appeared to be tripartite (Chen et al. 1999). Cambrian early vertebrates and their relatives may have already possessed brain divisions seen in living vertebrates, such as the hindbrain, midbrain, and forebrain with cerebral hemispheres (Shimeld and Holland 2000; Northcutt 2002; Chen 2008).

The Cambrian provides us with the first definitive evidence of brains in the fossil record, although neurons and nervous systems would

have been present earlier. Paulin and Cahill-Lane (2021) suggested that neurons evolved from epithelial cells in Ediacaran mat grazers, which first developed a need to process and respond to event-based sense data resulting from innovation in feeding and motility. Decentralized nervous systems in the form of diffuse nerve nets probably characterized much of the Ediacaran fauna according to Northcutt (2012), with ganglionated nervous systems possibly approaching brain-level organization for some animals with apparent cephalization (e.g., *Spriggina*), especially if they turn out to represent clades related to annelids or panarthropods. Northcutt (2012) also discusses the unresolved question of whether the last common bilaterian ancestor possessed a centralized brain or whether it had a simpler nervous system from which brains evolved multiple times independently. Likewise, Evans et al. (2021) consider, based on body plan-related characters in Ediacaran macrofossils, that the rudimentary nervous systems in early animal lineages persisted for a long while before separate developments of a central nervous system.

Feinberg and Mallatt (2013) and Barron and Klein (2016) argued that consciousness first appeared in the Cambrian when, with the onset of advanced brains, animals could neurally represent the external world and perceive themselves moving within it. Similarly, according to Trestman (2013), the diversification of animals with complex, active bodies during the Cambrian radiation itself was dependent on “embodied cognition”—spatial awareness and bodily perception and control—which allowed for agent-like actions, such as manipulating objects.

Behavioral evidence provides another view of the Cambrian information revolution, revealing how animals responded to received information from the environment and other individuals, and how they may have sent information to others in return. Numerous types of behaviors have been attributed to Cambrian animals (Table 1). Some of these lines of evidence reflect inferences from morphological adaptations to life modes (e.g., predation) that require certain behaviors, or features such as color patterns or ornamentation meant to signal and influence the behaviors of others. Other lines of evidence reflect the results of

behavior as preserved in trace fossils or in body fossils in life positions (e.g., hiding in enclosed spaces).

Though animals were already fully motile, leaving locomotion traces, in the Ediacaran (Evans et al. 2019; Ivantsov et al. 2019); the trace fossil record also speaks to a revolution in sensing, cognition, and behavior across the Ediacaran/Cambrian boundary. Carbone and Narbonne (2014) examined strata from north-west Canada spanning this interval, finding that trace fossils representing only simple sensory behaviors, like undirected horizontal traces and two-dimensional avoidance traces, dominated the Ediacaran, while the succeeding parts of the Cambrian (Terreneuvian) yielded traces showing more sophisticated, complex feeding behaviors like zigzag probing and vertical probing. A well-known example is the burrow *Treptichmus*, which defines the boundary between the Ediacaran and Cambrian periods (Vannier et al. 2010; Buatois 2018). Based on fossil to modern comparisons, treptichnids like *Treptichmus* have been linked to priapulid tracemakers (Vannier et al. 2010; Kesidis et al. 2019) that have nerve networks arranged in rings and longitudinally (Adrianov and Malakhov 2001); such nervous systems existing in the late Ediacaran are consistent with the ideas of Northcutt (2012) and Evans et al. (2021).

Following up on these studies, we explore how Cambrian faunas compare with later marine faunas in sensing and cognition to test the hypothesis that the Cambrian information revolution was a unique event in the history of metazoans. It may be that Cambrian ecosystems already achieved comparatively modern levels of complexity, with later changes being more modest. Alternatively, the sensory and cognitive complexity of animals in marine ecosystems may have continued to rise considerably, for a number of reasons. Heterogeneity that favors cognition (Plotnick et al. 2010) may have increased further as ecosystem structure became yet more complicated, with greater tiering (Bottjer and Ausich 1986; Droser and Bottjer 1989; Bush et al. 2007) and with the proliferation of complex, three-dimensional habitats such as reefs (Wood 1999). Through the Phanerozoic, biodiversity increased, which

TABLE 1. Behaviors, behavioral abilities, or morphological correlates of behavior inferred to exist by the Cambrian.

Behavior or behavior-related attribute	Taxa involved	Nature of evidence	Source
Associative learning	Many bilaterians	Phylogenetic inference	Ginsburg and Jablonka 2010
Hunting and searching	Arthropod predator, annelid prey	Trace fossils (burrows)	Pickerill and Blissett 1999
Selective predation, prey selectivity	Arthropod predators on arthropod prey; arthropod predator on annelid prey; unknown invertebrates with various invertebrate prey; unknown worm-like predator on arthropods and worm-like animals; unspecified predator on arthropods, priapulid <i>Othoia</i> on various invertebrates (counterexample, showing nonselective predation)	Fossil gut contents, trace fossils (burrows, coprolites, skeletal injuries), functional morphology	Zhu et al. 2004; Vannier 2012; Shen et al. 2014; Selly et al. 2016; Kimmig and Strotz 2017; Kimmig and Pratt 2018; Pates and Bicknell 2019
Left/right asymmetry, behavioral lateralization	Arthropods (trilobites) and their unknown predators	Trace fossils and morphology (bodily malformation/injuries)	Babcock 1993; Bicknell et al. 2019; Bicknell and Pates 2020
Vertical migration and hunting	Arthropod	Functional morphology	Vannier et al. 2009
Gregarious, collective behavior	Arthropods	Preserved body positions and spatial association	Hou et al. 2008; Xian-guang et al. 2009; Chambers and Brandt 2018
Synchronized molting, same-age cohort nursery	Arthropods	Preserved body positions and spatial association	Haug et al. 2013
Brooding	Arthropods	Functional morphology; preserved body positions and spatial association	Duan et al. 2014; Caron and Vannier 2016
Cryptic behavior, hiding in enclosed spaces	Arthropods	Preserved body positions and spatial association	Chatterton et al. 2003; Fatka and Szabad 2011
Color signals	<i>Canadia</i> (annelid), <i>Marrella</i> (arthropod), and <i>Wiwaxia</i>	Functional morphology	Parker 1998
Mimicry	Brachiopods (against unknown predator)	Functional morphology	Topper et al. 2015
Sexual signals and sexual dimorphism	Arthropods	Functional morphology	Zhang 1987; Cederström et al. 2011; Fu et al. 2014
Symbiosis—potential mutualism, commensalism, or parasitism	Brachiopods and priapulids, annelids and hemichordates, brachiopods and <i>Wiwaxia</i> , encrusting tubular organisms and <i>Vetulicola</i> , tube-dwelling organisms and brachiopods, vermiform animals and brachiopod, worm-like animals and larger host worms, various other invertebrates	Preserved body positions and spatial association	Bassett et al. 2004; Topper et al. 2014; Cong et al. 2017; Vinn 2017; Li et al. 2020; Zhang et al. 2020; Nanglu and Caron 2021; Yang et al. 2021

might lead to increased biotic interactions through higher rates of different kinds of animal detecting, encountering, and responding to one another, and thus an increased demand for cognition. For example, the great Ordovician biodiversification event produced enormous taxonomic and ecological diversification within phyla (Servais and Harper 2018), and Mesozoic radiations produced a “modern” fauna more diverse and ecologically complex than what existed before (Sepkoski 1981, 1984; Bush and Bambach 2015), including the sensorially and behaviorally rich vertebrates. All the while, the average biomass and metabolism of animals increased, energetic life modes became prominent (including mobile, specialized predators, and infaunal burrowers), and new kinds of escalation between predators and prey took place (Vermeij 1977, 1993; Bambach 1983, 1993; Bush et al. 2007; Knope et al. 2015; Smith et al. 2016), which could favor better sensory processing among metazoans alongside better physical offensive and defensive strategies.

We examine whether and to what extent the share of animals with complex sensory or information-processing systems increased in post-Cambrian marine ecosystems after the initial information revolution wherein many of these systems first appeared. We thus will place the Cambrian information or sensory revolution in the context of the rest of the Phanerozoic. We examine this question from three points of view. First, we compare the proportion of animals with macroscopic sense organs reflecting photoreception (eyes) and chemoreception (antennae, feelers, or nostrils) in well-known marine Lagerstätten from the Cambrian and post-Cambrian, as well as one modern marine fauna (cf. Plotnick et al. 2010; Zhao et al. 2013). Possession of both types of (typically paired) organs allows for increased sensory acuity as well as spatial perception of the stimulus (Plotnick et al. 2010). Lagerstätten were chosen because their high-quality preservation allows a wider taxonomic census; they are also heavily researched and have readily available published genera or species lists in academic papers and/or field guidebooks.

Second, for the same set of faunal assemblages, we infer the proportion of animals

with four different levels of nervous system complexity: (1) no neurons, thus no nervous system; (2) decentralized nervous system (e.g., nerve net or ring); (3) nervous system with ganglia, but no brain; and (4) nervous system with a centralized brain. These levels represent grades in organization of information processing and can be applied to fossil taxa by comparison with modern analogues and their body plans.

Finally, we determine which ecological life modes and areas of ecospace are associated with these four grades of neurological complexity using the scheme of Bambach et al. (2007) and Bush et al. (2007). This allows us to consider whether certain lifestyles require or favor more well-developed information-processing systems than others, both in the Cambrian and today.

## Methods

*Lagerstätten Faunas.*—We compared 23 faunal lists, 22 from famous and well-described marine Lagerstätten (14 Cambrian, 8 post-Cambrian) and one from a guidebook representing a modern marine fauna (Bermuda). Fossil faunal lists came from the published literature and field guidebooks (see Supplementary Data). For each faunal list, we tallied the proportion of metazoan genera present that had or are inferred to have had macroscopic photoreceptive organs (eyes) and macroscopic chemoreceptive organs (antennae, feelers, or nostrils).

The 14 Cambrian Lagerstätten faunal lists include the major Burgess Shale-type (BST) biotas—the Chengjiang, Sirius Passet, Sinsk, Guanshan, Balang, Emu Bay, Kinzers, Kaili, Spence, Burgess Shale, Wheeler (House Range), Wheeler (Drum Mountains), Marjum and Weeks (Foster and Gaines 2016; Holmes et al. 2018). The post-Cambrian Lagerstätten include the Ordovician-aged Fezouata (Van Roy et al. 2015) and Soom Shale (Gabbott et al. 2017), Devonian Hunsrück (Südkamp 2017) and Carboniferous Mazon Creek (Wittry 2012), the Jurassic La Voulte-sur-Rhône (Charbonnier et al. 2014), Oxford Clay (Martill and Hudson 1991) and Solnhofen (Bartel et al. 1990), and the Eocene London Clay (Rayner 2009). The one modern faunal list comes from

Bermuda (Sterrer and Schoepfer-Sterrer 1986), a region well studied and surveyed across all major taxonomic groups by generations of marine biologists (Beers 1963). This well-described contemporary ecosystem provides a useful comparison to our well-described fossil ones. Although these assemblages differ in preservational mode and history of study, which adds inevitable variability to our analyses, we consider using these well-studied Lagerstätten to be the closest to lifelike censuses of ecosystems possible among fossil assemblages, including many taxa that would otherwise not be preserved.

We restricted our analysis to marine organisms, except for the Mazon Creek, for which the freshwater to saltwater transition is not clearly defined. For this Lagerstätte, we included all aquatic taxa. Overall, we included marine reptiles, marine mammals, and amphibians, but excluded flying seabirds or pterosaurs. For consistency with the fossil assemblages, we also excluded the small phyla Tardigrada, Gnathostomulida, Gastrotricha, Rotifera, and Kinorhyncha, as well as internal parasites (e.g., tapeworms, acanthocephalans), from the modern Bermuda fauna. These animals had limited preservational potential in our fossil assemblages, although there may be occasional examples of them elsewhere in the fossil record. Trace fossil taxa were also excluded. The number of genera used in each Lagerstätte for each of the anatomical comparisons is shown in Table 2.

*Sensory Organs.*—Animals were coded as having eyes if there were macroscopic visual organs. Macroscopic chemoreceptive organs include the antennae of arthropods and polychaetes, the paired feelers or tentacles of gastropods, and the nostrils of chordates. Because many of these anatomical traits are rarely preserved, several lines of evidence were used for the coding, both direct and indirect. Anatomical traits were examined from descriptions in published papers and guidebooks, including any photos, figures, or reconstructions. If these were not available, traits were assigned to the fossil genera within crown groups known to possess them in the modern (e.g., crustaceans have antennae, except for known cases where they have been lost, like barnacles; all sponges lack sense organs or nervous systems). Taxonomic information for such coding

was generally taken from the published sources of the faunal lists if available, or from online sources such as the Paleobiology Database, though this was not done for highly disputed or uncertain taxonomic assignments. Genera for which the anatomical assignment was too uncertain were excluded from the analyses (e.g., unclear preservation of the feature or belonging to extinct phyla without clear modern analogues). These make up a noticeable minority of nearly all analyzed Cambrian and Ordovician faunal lists (e.g., typically 10%–20%, but up to slightly over a third), but had limited effect on the later faunas (uncertain coding only existed in Hunsrück and Mazon Creek genera, making up <10%, and mostly in annelid sense organs).

*Nervous System Complexity.*—We also classified metazoan taxa in the same set of faunal assemblages into four major categories of nervous system complexity based on the published literature and invertebrate zoology textbooks. The first category includes multicellular organisms without nervous systems (i.e., sponges). Although they are able to respond to stimuli, they do not have specialized information-relaying cells (i.e., neurons) that directionally pass electrochemically encoded signals around the body much faster than typical chemical diffusion (Nickel 2010). The second category includes animals with decentralized nervous systems, like cnidarians and echinoderms. Neurons are positioned in tracks reaching to and from various parts of the body (nerve nets or rings). The third category includes animals that possess ganglia, which are clusters or bundles of nerve cells that help organize sensing and action by controlling different processes or different areas of the body. The fourth category includes animals in which the nervous system is further organized and centralized into a major organ, the brain, which is located anteriorly and often near major sense organs. The brain sends and receives signals to and from the rest of the body, which is thought to be necessary for coordinating complex, active bodies with large behavioral repertoires (Trestman 2013).

As with sense organ anatomy, but even more so, nervous systems are only very rarely directly fossilized, so we have relied on inference

TABLE 2. Total number of genera in each Lagerstätte or other faunal assemblage examined and number of genera that could be scored for the absence or presence of eyes, chemoreceptive organs, and type of nervous system. Some taxa were excluded from scoring based on reasons such as unclear preservation or uncertain or disputed taxonomic assignment.

Lagerstätte	Number of genera examined	Number of genera scored for absence or presence of		
		Eyes	Chemoreceptive organs	Nervous system
Chengjiang	226	172	168	180
Sirius Passet	40	36	38	30
Sinsk	36	32	32	31
Guanshan	53	45	45	42
Balang	34	31	31	24
Emu Bay	22	22	21	17
Kinzers	23	18	18	17
Kaili	113	101	97	96
Spence	74	68	68	64
Burgess	194	177	172	166
Wheeler (House Range)	53	48	48	48
Wheeler (Drum Mountains)	56	46	47	51
Marjum	77	70	70	70
Weeks	50	48	45	46
Fezouata	148	115	120	131
Soom	21	15	15	19
Hunsrück	167	160	162	162
Mazon Creek	139	130	139	139
La Voulte-sur-Rhône	50	50	50	50
Oxford Clay	167	167	167	167
Solnhofen	186	185	185	186
London Clay	230	230	230	230
Modern Bermuda fauna	968	968	968	968

based on modern analogues and representatives of taxonomic groups. Body plans are highly conserved among phyla or classes within phyla, and nervous system organization, at least on a broad level, is often tightly correlated with aspects of body plans (Evans et al. 2021)—for instance, possession of an anterior-posterior axis, cephalization, appendages, and muscles. Most of our fossil genera could be assigned to at least the phylum level, where these traits are inferable, though the share is smaller for Cambrian ones, as discussed later on. Nonetheless, we acknowledge these types of paleobiological analyses will always have some uncertainties, although the same is true of many other studies. Because nervous system complexity is tightly correlated with phylogeny, trends in nervous system complexity will reflect trends in the taxonomic composition of the fauna. However, this does not mean that these trends are not worthy of examination. Nervous system complexity influences an animal's ability to manipulate its environment, interact with other species, and respond to stimuli, so these trends have important implications for ecology and evolution, even if

they are tied to taxonomy. A similar approach has been used in studies of respiratory and circulatory system organization (Heim et al. 2020), vision (Aberhan et al. 2012), reproductive mode (Bush et al. 2016), and even life modes such as motility (Bush et al. 2007).

Brains were inferred in the chordates, arthropods, stem-arthropods, lobopodians, cephalopod and gastropod mollusks, and some annelids. Among annelids, polychaetes having sense organs and active life modes were generally considered to have brains, whereas other annelids generally were coded as ganglia-only; this is a judgment based on the complexity of the nervous system in members of the phylum today (Beesley et al. 2000; Rouse and Pleijel 2001; Orrhage and Müller 2005; Heuer et al. 2010). Additionally, to examine the taxonomic distribution of brains in each fauna, we calculated the relative proportion of brain-bearing genera belonging to the following taxa: chordates, panarthropods (arthropods and their relatives, including lobopodians), cephalopods, gastropods, and annelids.

*Statistical Comparison.*—To test whether Cambrian and post-Cambrian assemblages

were different in proportions of eyes, chemoreceptive organs, and brains, we performed a two-step resampling routine run with 10,000 iterations. We resampled the genera in each assemblage with replacement at the original sample size (number of genera), calculating the proportion possessing the anatomical trait for each iteration. Then, to calculate the mean proportion for each interval (Cambrian and post-Cambrian), we resampled the assemblage-level means with replacement at the original sample size (number of assemblages). The Cambrian mean was subtracted from the post-Cambrian mean for comparison—there would be a significant difference between the two intervals if the 95% confidence interval did not overlap zero.

*Life Modes and Nervous System Complexity.*—To examine the relationships between our four levels of nervous system complexity (no neurons, decentralized system, ganglia, or brain) and ecological modes of life, we used the ecospace scheme of Bambach et al. (2007), which categorizes marine animals with respect to three parameters—tiering relative to the sediment–water interface, motility level, and feeding mechanism. Six possible values for each parameter exist, with each combination of the three parameters defining a unique life mode; the resulting ecospace is depicted as a cube (Fig. 1). Not all of the 216 theoretical life modes are employed by known organisms, such that not all of the theoretical ecospace is actually filled. Bambach et al. (2007) and Bush et al. (2011) examined which parts of ecospace were actualized in the Recent and at other times in the history of animal life.

We use the data in Bambach et al. (2007) and Bush et al. (2011) to evaluate which life modes (and thus extent of ecospace occupation) are associated with our four types of nervous system in animals in the Recent and the Cambrian. The data were restricted to the major phyla, including the larger soft-bodied “worm” phyla but excluding minor, small-bodied taxa such as rotifers and placozoans. The taxa we included for each level are as follows: (1) no nervous system—Porifera; (2) decentralized nervous system—cnidarians, ctenophores, echinoderms, hemichordates, priapulids, and

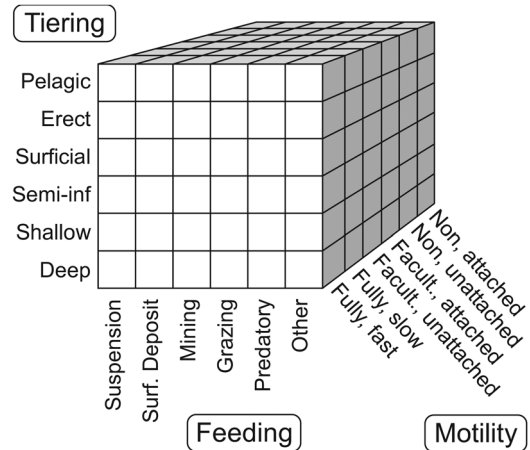


FIGURE 1. Theoretical ecospace of marine animals, from Bush et al. (2007), with the three ecological parameters of tiering, motility level, and feeding mechanism. Definitions of the individual categories within each parameter are also in Bambach et al. (2007) and Bush et al. (2007).

brachiopods; (3) ganglia—bryozoa, non-gastropod, non-cephalopod mollusks, non-polychaete annelids (including pogonophorans and echiurans in the annelids), sipunculids, nemerteans, “platyhelminth” flatworms, and nematodes; and (4) brain—all chordates, panarthropods, gastropods, cephalopods, and polychaetes. This is generally similar to how they were coded for our Lagerstätten comparison analysis. Cambrian taxa excluded because they could not be assigned to a nervous system type include anabaratids, cambroclavids, cancellorids, coeloscleritophoans, decollating tubular fossils, halkierids, hyolithelminthes, hyoliths, protoconodonts, stenothecoids, tommotids, vetulicolians, and trace fossils, plus those labelled “problematica” and not assigned to a phylum. These excluded taxa had 15 life modes among them, but of these, all but two (possessed by anabaratids and decollating tubular fossils) were inhabited by Cambrian taxa included in the analysis.

## Results

*Lagerstätte Faunas.*—The proportion of genera bearing eyes (Fig. 2A) across the 19 faunas ranged from 24% (Sirius Passet) to 83% (London Clay). On average, across all faunas, around half of the



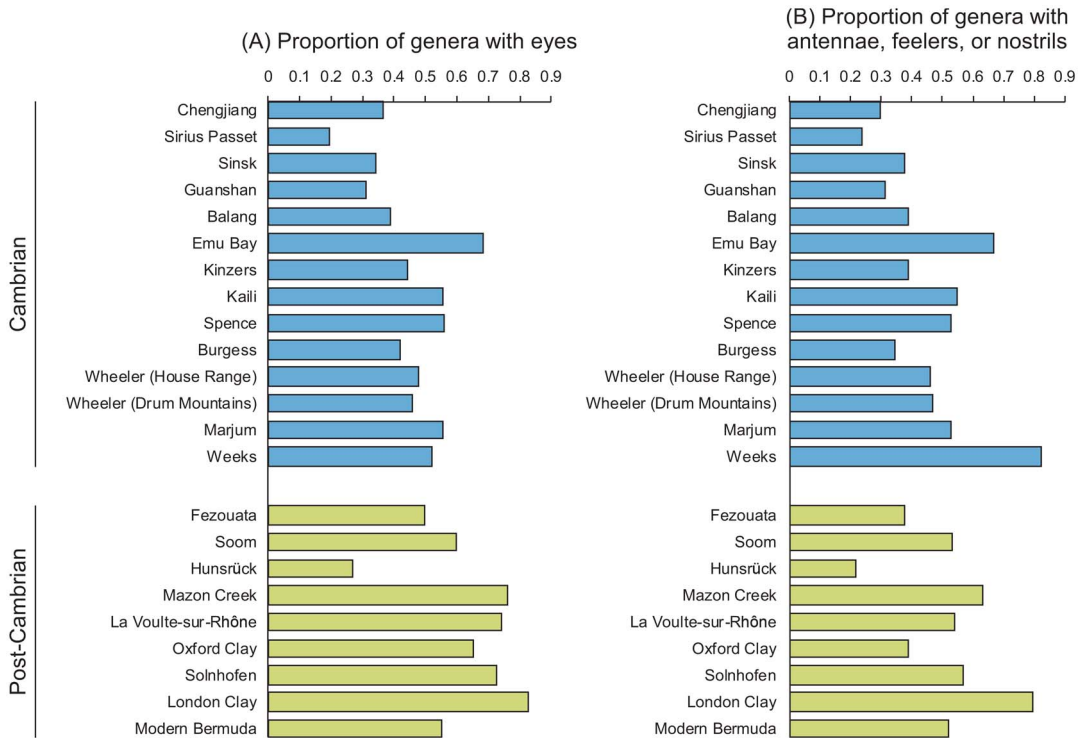


FIGURE 2. Proportion of listed genera in each fauna possessing macroscopic sense organs. A, Eyes. B, Chemoreceptive organs—antennae, feelers, or nostrils.

genera had eyes. Cambrian faunas had 45% of genera with eyes on average, compared with 62% in the post-Cambrian. The average difference between the post-Cambrian and Cambrian was 18%, which was statistically significantly different from zero, with a confidence interval of [3%, 31%]. Thus, there was a significant increase in the mean proportion of eyes.

The proportion of genera bearing macroscopic chemoreceptive organs (antennae, feelers, or nostrils) across the 19 faunas ranged from 22% (Hunsrück) to 82% (Weeks) (Fig. 2B). On average, across all faunas, 48% of the genera had these chemoreceptive organs. Cambrian faunas had 45% of genera with these organs on average, compared with 51% in the post-Cambrian. The mean percentage of genera with chemoreceptive organs was not statistically significantly different in the post-Cambrian and Cambrian, with the confidence interval on the difference being [−10%, 20%].

In most faunas, the majority of genera had centralized brains—on average 65% in the

Cambrian faunas and 66% in the post-Cambrian (Fig. 3A). The difference between the post-Cambrian and Cambrian was not significant, with a confidence interval of [−12%, 14%]. The average share of genera with ganglion-level organization was lower in the Cambrian (<1%) than the post-Cambrian (11%), with bivalves and bryozoans contributing heavily to the post-Cambrian value. The low Cambrian value might partly reflect uncertainty in assigning genera to this category compared with the three others. Decentralized nervous systems were possessed by 22% of the Cambrian faunas on average, with a similar 21% in the post-Cambrian. Finally, 12% of genera had no nervous system in the average Cambrian fauna, reflecting a diversity of sponges, compared with only about 2% in the post-Cambrian.

Even though the average proportion of genera with brains was similar in Cambrian and post-Cambrian faunas, there is a notable difference in which taxonomic groups make up the

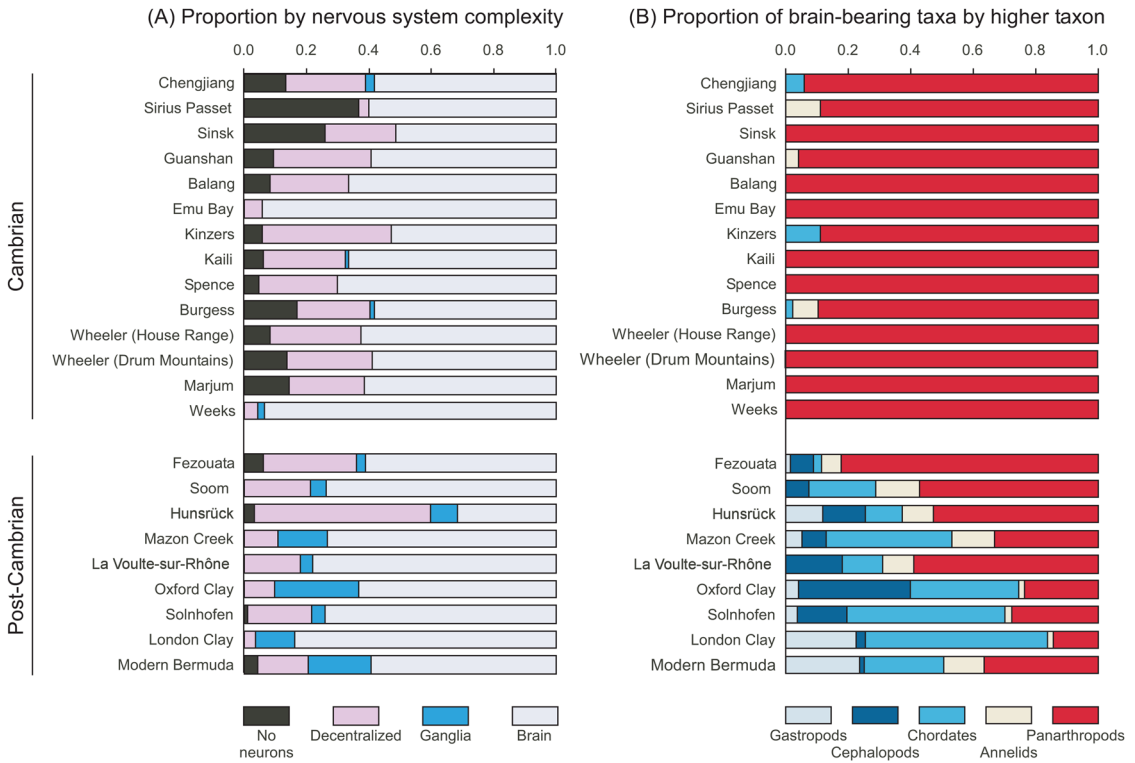


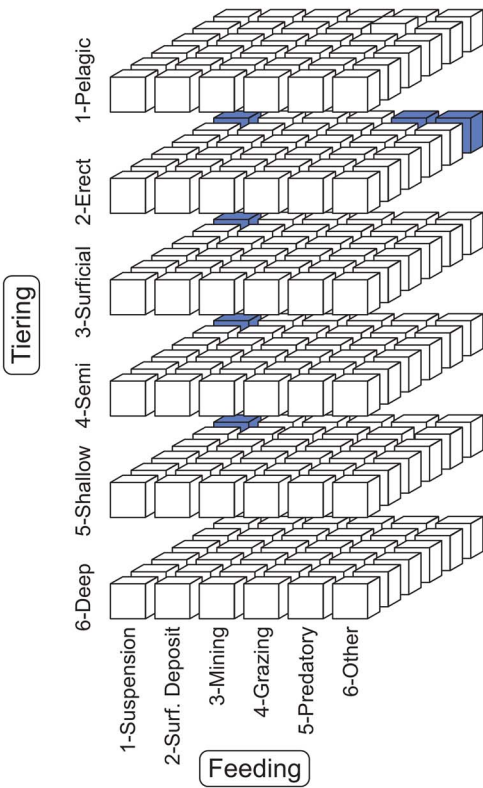
FIGURE 3. Nervous system complexity. A, Proportion of listed genera in each fauna by level of nervous system complexity. B, Proportion of genera that possess brains that belong to each major taxonomic group.

genera with brains (Fig. 3B). Cambrian genera with brains are overwhelmingly panarthropods (89%–100%), with the remaining genera being annelids or chordates. Nine of the 14 Cambrian faunas have panarthropods as the only animals with brains. By contrast, the post-Cambrian faunas surveyed are more diverse in brain-bearing taxa—the majority have representatives of the chordates, panarthropods, cephalopods, gastropods, and annelids. The transition to this more diverse set of brain-bearing taxa can be seen in the two Ordovician faunas. In the Early Ordovician Fezouata biota, 83% of genera with brains are still panarthropods, but small shares of chordates, cephalopods, gastropods, and annelids are also present. Later in the Ordovician, only 57% of brain-bearing genera are panarthropods in the Soom Shale. While a single major taxon dominates the brain-bearing genera in some post-Ordovician faunas (i.e., La Voulte-sur-Rhône and Hunsrück have slight panarthropod majorities, and the London Clay and Solnhofen have

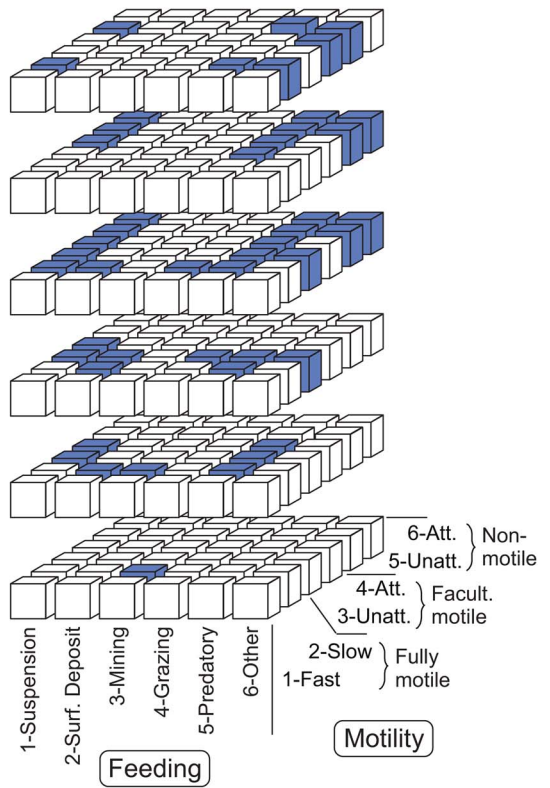
slight chordate majorities), no group overwhelmingly dominates among the brain-bearing taxa in these later faunas the way panarthropods did in the Cambrian and Early Ordovician.

*Life Modes and Nervous System Complexity.*—Among the major taxa we examined, 6 ecological modes of life are occupied in the Recent by genera with no nervous system, 47 by those with decentralized nervous systems, 41 by those with ganglia, and 60 by those with a brain (Fig. 4). Thus, metazoans with no nervous system (i.e., Porifera; Fig. 4A) occupy much less ecospace than metazoans with a nervous system of any kind (Fig. 4B–D). The few life modes occupied by the former group are characterized by a lack of motility, and they occupy only a few tiers and a few feeding modes, mainly suspension feeding. With even a decentralized nervous system (Fig. 4B), animals can move around, occupying all but the most active of the six motility categories (fully motile fast); they can also occupy all six tiers and all six

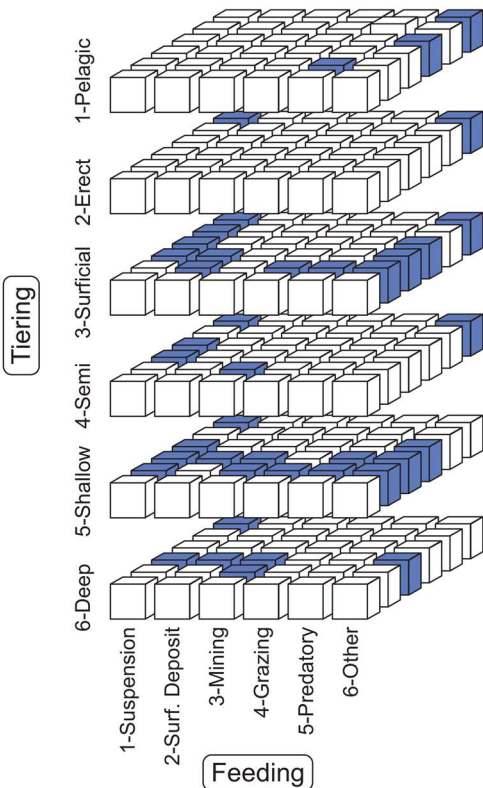
(A) No nervous system



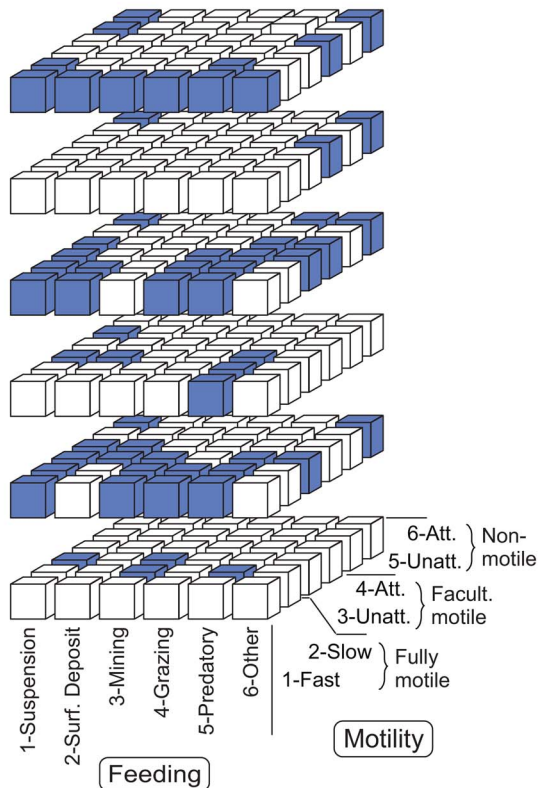
(B) Decentralized nervous system



(C) Ganglia



(D) Brain



←  
 FIGURE 4. Life modes associated with each of the four levels of nervous system complexity in the Recent. A, No nervous system. B, Decentralized nervous system. C, Ganglia. D, Brain.

feeding categories. Animals with ganglia are similar in this range of ecospace occupation (Fig. 4C). Much of this ecospace continues to be used by animals with brains (Fig. 4D), but only the brain-bearing animals occupy the “fully motile fast” category (Fig. 4D, front rows closest to viewer in diagram). This category involves regular rapid and unencumbered movement, such as walking or swimming (and which differs from “fully motile slow,” whereby routine movement retains more of a bond with substrates, such as creeping or gliding). A borderline exception may be the chaetognaths (not included in figures), small fast predators on plankton that have existed since the early Cambrian (Vannier et al. 2007), which we might code as having ganglia rather than a well-developed brain, because their cerebral ganglion is one of multiple ganglia in the central nervous system (Harzsch and Wanninger 2010).

In the Cambrian (Fig. 5), 4 ecological modes of life are occupied by animals with no nervous system), 17 by those with a decentralized nervous system, 8 by those with ganglia, and 15 by those with a brain. Although there are fewer modes of life overall (as seen in Bambach et al. 2007; Bush et al. 2011; Knope et al. 2015), the relationship between nervous system development and ecospace occupation that is found in the Recent is already developed. Specifically, metazoans without neurons are associated only with the lowest motility category and with limited tiering and feeding mechanisms; possessing a nervous system—even a decentralized one—is linked to major expansion into additional motility levels, tiers, and feeding modes. Also, brains are associated with the occupation of the fully motile fast life modes.

There was an ecospace increase between the Cambrian and Recent for all four levels of neurological complexity, reflecting the continued Phanerozoic ecological diversification of many metazoan phyla past their initial Cambrian appearances. Though only slight increase is seen in the neuron-less sponges, the three categories possessing nervous systems all more

than double their number of life modes. The close to tripling of life modes for decentralized nervous systems is associated with the ecospace expansion of cnidarians and echinoderms, and the fivefold and fourfold rise in life modes for ganglia and brains, respectively, is associated with those of numerous other bilaterians. Though there is some difference and lag in which regions of ecospace were occupied first (for instance, animals with decentralized nervous system reach all tiers in the Cambrian, earlier than those with ganglia or brains do), by the Recent, all three nervous system categories end up occupying very similar regions of ecospace aside from the additional region of “motile fast” ecospace held by brains alone.

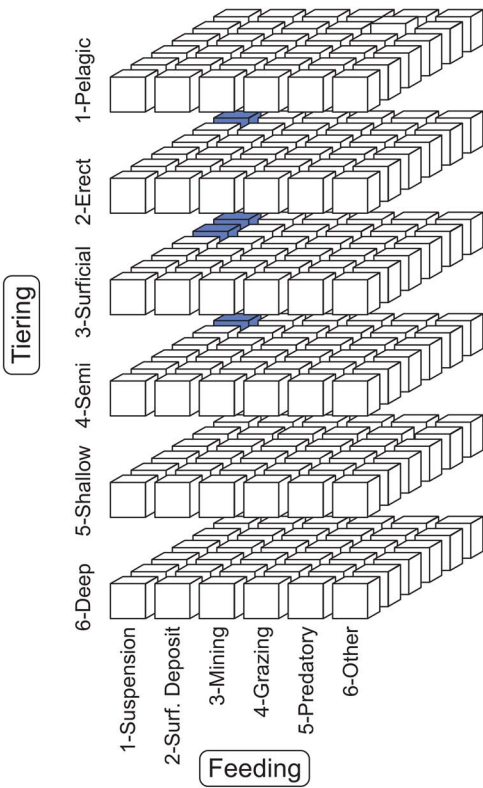
Arthropods were the most varied in life mode among the groups with brains, although all brain-bearing taxa ecologically diversified to a major degree, with many of their life modes overlapping. In the Cambrian, arthropods occupied 10 of the 15 life modes possessed by animals with brains, polychaetes occupied 3, while gastropods, cephalopods, and chordates each occupied only 2 life modes. Among the 60 Recent life modes occupied by animals with brains, arthropods possess 42; chordates, 26; polychaetes, 23; gastropods, 15; and cephalopods, 4.

From the Cambrian to the Recent, the number of life modes in the most active, fast-moving category, which as previously mentioned are nearly exclusively linked to brains, nearly quadrupled, from 4 to 15. Arthropods held all (and chordates held 1) of the 4 Cambrian fast life modes, while more groups comprised the 15 Recent fast life modes—arthropods (13 modes), chordates (9 modes), cephalopods (2 modes), and polychaetes (1 mode).

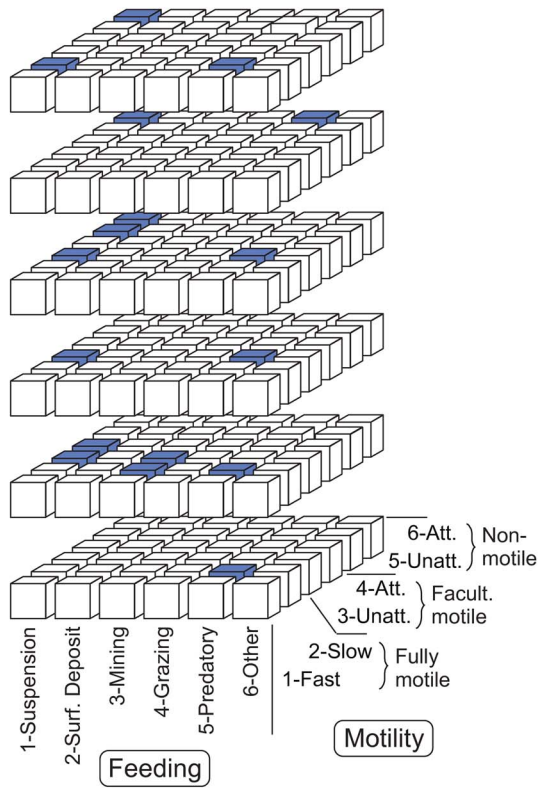
## Discussion

Our results support the idea that Cambrian ecosystems were very “modern” in the proportion of animals capable of information processing as reflected through their anatomy, comparable to those later in the Phanerozoic. Sense organs were abundant across most of

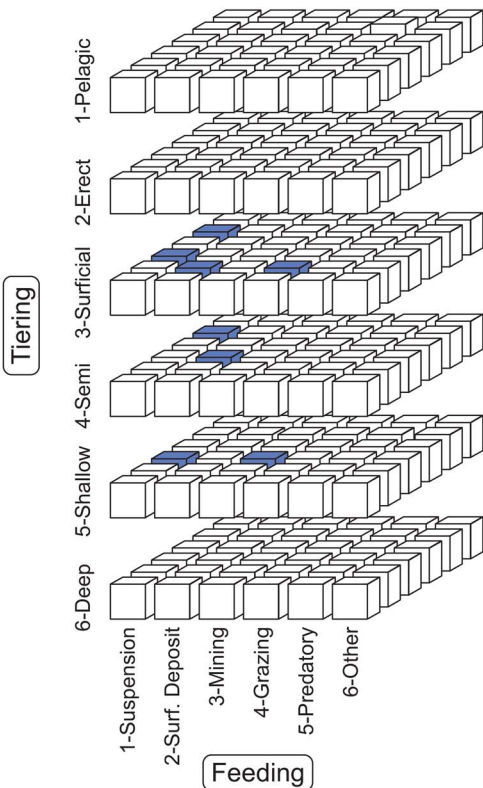
(A) No nervous system



(B) Decentralized nervous system



(C) Ganglia



(D) Brain

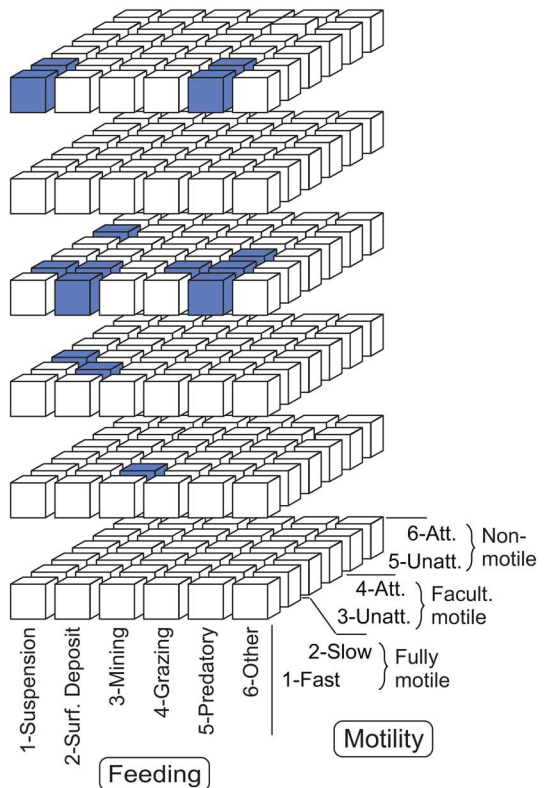


FIGURE 5. Life modes associated with each of the four levels of nervous system complexity in the Cambrian. A, No nervous system. B, Decentralized nervous system. C, Ganglia. D, Brain.

the faunas we examined, with post-Cambrian ecosystems on the whole averaging more, particularly for eyes, due to the addition of cephalopods and chordates as major components of the fauna. Cambrian and post-Cambrian faunas had similar percentages of genera with brains, with all but one fauna having more than 50%, implying marine ecosystems had high cognitive complexity through much of the Phanerozoic. The high proportion of both types of sense organs alongside brains is expected, as these traits covary—brains are needed to process input from the senses, and vision and chemoreception can be strongly complementary for many animals engaging in active navigation (Plotnick et al. 2010). In the Cambrian, as in the present, the presence of a nervous system in marine animals was associated with occupation of diverse habitat tiers, feeding modes, and motility levels. However, the most active life modes—those classed as fully motile fast—are almost exclusively associated with brain-bearing animals, suggesting such lifestyles require the fast information-processing abilities and muscular responses associated with a centralized nervous system. Information-processing ability is expected to be a major constraint on the potential to enter or radiate within certain regions of ecospace, even if many life modes can be occupied by animals with varying levels of neurological complexity. For instance, epifaunal grazer roles can be filled by eyeless, brainless sea urchins as well as cephalized snails, while nerveless sponges and ganglionated bivalves alike act as reef builders in different time periods. However, no fast-moving swimming predators in the manner of anomalocarids or dolphins exist among the brainless. In the Cambrian, complex sensory and nervous systems were concentrated in a single major taxon, the (pan)arthropods, whereas later faunas had a more diverse set of sensorially and cognitively complex groups, with chordates and mollusks becoming important constituents of the fauna.

Cambrian and post-Cambrian faunas overlap heavily in the proportion of genera with

sense organs or brains. Some of the variation in these proportions may be habitat related; for example, the two faunas with the lowest share of animals with eyes represent deeper-water habitats. The Sirius Passet fauna is reconstructed as having lived below the photic zone (Hammarlund et al. 2019; Harper et al. 2019), and the Hunsrück Slate was deposited at the least below storm wave base (Brett and Seilacher 1991; Sutcliffe et al. 1999). The Hunsrück was also the only one we analyzed in which a majority of the genera were inferred to lack brains.

Our comparison of Cambrian and post-Cambrian faunas is complicated by the exclusion of genera with uncertain anatomical coding, which are concentrated in the Cambrian. Our results may be biased in favor of greater Cambrian sensory and nervous system complexity if the excluded uncertain genera disproportionately lacked the more complex traits. If we reanalyze the data with all uncertain codings set to represent lack of eyes, antennae, and brains (which we consider very unlikely), the average faunal list in the Cambrian drops from 45% to 40% of genera having eyes, from 45% to 40% having the inferred macroscopic chemoreceptive organs, and from 65% to 54% having brains. This nonetheless still represents a large share with complex sensory and nervous systems, showing the importance the Cambrian information revolution had in bringing about very “modern” levels of information processing.

Though we focus on the large share of brain-bearing fauna, two other patterns for the other nervous system levels are worth mentioning—the decrease in the neuron-less category (sponges) post-Cambrian and the rise in the ganglionated one. Sponges, previously noted to be among the largest components of BST faunas (Botting and Peel 2016), are considered the dominant Cambrian sessile suspension feeders (Wu et al. 2014), and their proportional importance may have dropped as other animals radiated, including those taking similar niches. For instance, they are present but a minor

component of the ecologically diverse and well-sampled living Bermuda fauna in our data. However, a lack of sponges in some Lagerstätten may also reflect difficulty of preservation, as they often fall apart as isolated spicules. Some of the BST Cambrian Lagerstätten may be better at capturing them intact. The rise of ganglionated taxa heavily reflects the radiation of bivalves and bryozoans, which were absent or rare in the Cambrian faunas, though we also consider some potential underrepresentation of ganglionated Cambrian invertebrates among the excluded “problematica” based on uncertain coding (well-cephalized groups like arthropods and decentralized ones such as echinoderms were perhaps more clearly assigned to their nervous system level). A Phanerozoic increase in ganglionated animals relative to those with simpler nervous systems might also reflect an increase in motile benthos able to respond to disturbance (Bush et al. 2007; Manojlovic and Clapham 2021), a change expected to increase at least some information-processing abilities.

As with any ecological analysis performed with fossil data, there is always the consideration that taphonomy may obscure the original biological trends of interest. Though they include many soft-bodied or poorly mineralized taxa and allow much more complete ecosystem reconstructions than most other fossil assemblages, the Lagerstätten we examined would still miss many elements of the in-life fauna or have them altered by decay and transport (Caron and Jackson 2006; Nanglu et al. 2015). For instance, although BST deposits contain exceptionally preserved priapulids and polychaetes, they lack the even softer nemertean or flatworms (Butterfield 2003), which are recorded in the modern Bermuda faunal list. The sporadic distribution of Lagerstätten across time and space, as well as the potential unusualness of the paleoenvironments they represent, has frustrated their use in ecological or evolutionary analyses (Butterfield 1995, 2003; Gaines 2014). In addition, different Lagerstätten can have rather different preservational biases (Allison 1988; Saleh et al. 2020), adding noise to our analyses. Nonetheless, despite the great variability in (paleo)environments, preservational mode and history of study for

our 23 faunal assemblages across the Phanerozoic, it is noteworthy that the Cambrian and post-Cambrian faunas are so similar on average in the sensory and cognitive attributes we examined. Likewise, the modern Bermuda fauna was sampled and studied in a completely different manner, yet it displays reasonably similar statistics to the average fossil assemblage. This suggests a major underlying macroecological pattern could be present. Although we only analyzed one modern faunal list, modern biodiversity censusing of the world’s oceans has shown that three groups well represented in sensory and cognitive complexity—crustaceans, mollusks, and fish—are estimated to make up close to half the living species in most geographic regions (Costello et al. 2010).

Overall, our results underscore the importance of the Cambrian information revolution. The change in share of animals with complicated sensory and nervous systems between the Cambrian and post-Cambrian is minor compared with the relatively rapid evolution and development of information-processing systems in animals during the late Ediacaran–Cambrian transition. Fossils in the Ediacaran period have so far lacked macroscopic sense organs (Marshall 2006), and evidence for cephalization or brains is uncertain (Northcutt 2012), in stark contrast with all Phanerozoic ecosystems. This does not mean, however, that Ediacaran animals completely lacked sensory and nervous systems before the Cambrian information revolution. Evidence in the late Ediacaran of possible trackways of bilaterians walking with paired appendages (Chen et al. 2018), selective drilling by unknown predators (Hua et al. 2003), as well as the mollusk-like *Kimberella* and its feeding and locomotion traces (Gehling et al. 2014; Ivantsov et al. 2019) attest to at least rudimentary information-processing systems. Although the complexity of these systems remains unknown, they were sufficient to seek resources with directed locomotion and to manipulate food.

Due to the uncertainties involved, we did not attempt to quantify the neurological complexity of Ediacaran faunas in the same way as Phanerozoic faunas, though as previously mentioned, it is likely that at least diffuse nerve nets existed (Northcutt 2012). In any

case, the major development of bilaterian body plans that include recognizable sense organs and brains did not arise until the Cambrian radiation, even if these innovations relied on developmental tool kits that existed earlier in the Neoproterozoic (Erwin 2020). Although our Lagerstätte-based analysis begins temporally with the Chengjiang and Sirius Passet faunas in Cambrian Stage 3, complex sense organ-bearing and brain-bearing taxa were expanding earlier in the Cambrian, as the trace fossil record attests (Carbone and Narbonne 2014; Mángano and Buatois 2020). Specifically, the continuous trace fossil record across this interval records the behaviors of sensorially and cognitively complex bilaterians, including euarthropods, that would come to dominate the body fossil assemblages sampled in our analyses (Mángano and Buatois 2020).

All in all, evidence suggests that new ways of sensing, processing, and responding to information developed early in marine ecosystems in the Cambrian information revolution, as anatomical data reveal their already widespread presence by Cambrian Stage 3. Subsequent to the Cambrian, more sophisticated variants of these systems evolved, but change was a matter of degree rather than kind (e.g., there were increases in the acuity of eyes or processing power of brains in many lineages). This is somewhat analogous to how most phyla and body plans were present by the Cambrian, with diversification and elaboration happening within them later. We can also compare our results with Aberhan et al.'s (2012) previous findings that the proportional diversity of marine invertebrate genera possessing vision peaked early in the Phanerozoic, continuing at a lower, stable level after the Ordovician. Because we included chordates, we find the share of eyes in marine assemblages to somewhat increase post-Cambrian (excluding chordates, the increase in the share is smaller, with an 11% rather than an 18% difference in proportion between Cambrian and post-Cambrian, and the two intervals would not significantly differ statistically by our resampling test). Our results also differ from those of Aberhan et al. (2012) in finding overall higher shares of eye-bearing genera across the Phanerozoic, possibly because we examined data from select

Lagerstätten and a modern assemblage, where they might be more easily recorded than in most fossil assemblages. No or little rise in the average post-Cambrian share of the fauna with macroscopic sense organs and brains might represent “saturation” of ecospace or of life modes where sensory and cognitive complexity is required, consistent with Bush et al.'s (2011) findings that much of modern ecospace in terms of tiering, motility, and feeding modes was already occupied by the Cambrian. Similarly, Dunne et al. (2008) showed that Cambrian food webs are very similar to modern ones. There may be only so many niches in an ecosystem that require complex cognition, at least in proportional terms. This would be consistent with such a similar average share of genera (around two-thirds) possessing brains in our analysis for both the Cambrian and post-Cambrian in spite of such a great shift in the balance of which taxonomic groups possessed them through the Phanerozoic. Similarly, the largest rise in diversity of trace fossils occurs during the Cambrian radiation, with later increases more modest or gradual, as found by Buatois and Mángano (2018).

Future research could also examine changes in the complexity of macroscopic sense organs or brains over the Phanerozoic, in addition to their presence or absence. For instance, the neural architectures seen in Cambrian panarthropods (Ma et al. 2012; Tanaka et al. 2013; Cong et al. 2014; Strausfeld 2015) are quite conserved and similar in complexity to those in the present. Likewise, Ma et al. (2012: p. 258) characterize compound eyes in the Cambrian as being “in size and resolution, equal to those of modern insects and malacostracans.” Such inference about Cambrian compound eyes is seen, for instance, from Paterson et al.'s (2011, 2020) finding that the stem-arthropod *Anomalocaris* compared well to most living arthropods in eye size, high ommatidial lens count per eye, and low interommatidial angles, all factors that correlate with visual acuity in the present. These claims would imply that modern levels of cognition and sensory acuity were achieved exceptionally early for arthropods. However, the situation may be different for chordates or cephalopods, with many large-brained and behaviorally sophisticated examples only



appearing or diversifying later in the Mesozoic and Cenozoic (e.g., teleosts, cetaceans, and coleoids). These animals probably have far more sophisticated nervous systems than their Cambrian ancestors, and they typically occupy more active life modes; small-brained Cambrian chordates were suspension feeders but not yet predators, and Cambrian cephalopods were slowly motile rather than fast motile. In contrast, Cambrian arthropods already occupied both fast and predatory life modes (based on data from Bambach et al. 2007).

Living non-vertebrate chordates (urochordates and cephalochordates) are reported to have only  $10^2$ – $10^4$  neurons in their brains, whereas vertebrates have  $10^7$ – $10^{14}$  (Meinertzhagen 2010). (For context, annelid brains have  $10^3$ – $10^4$  neurons; arthropod brains,  $10^5$ – $10^6$ ; and mollusk brains,  $10^3$ – $10^8$ ; with gastropods occupying the lower end of the range and cephalopods the upper end.) There is a long history of interest in the idea of a directional trend in cognitive evolution for vertebrates, although much of the literature pertains to terrestrial tetrapods. Russell (1981, 1983) noted that for animals (mostly vertebrates), average maximum encephalization, or proportional brain mass, increased through the Phanerozoic. He suggested that this was an example of “exponential evolution” or acceleration in biological complexity. Jerison (1970, 1973) also chronicled a gradual, progressive brain-size rise through the Mesozoic and Cenozoic among vertebrates.

Even if the proportion of animals with brains did not trend appreciably through the Phanerozoic, it is possible that there are more neurons firing in modern marine ecosystems than in Cambrian ones, which lacked big-brained vertebrates and cephalopods. One might expect that the prevalence of sensory and nervous systems is similar over time in similar niches, but with systems becoming more finely honed by pressures like predator–prey escalation. However, in some cases, novel sensory modes such as echolocation in cetaceans arose later in the Phanerozoic. Future research might examine temporal trends in the presence and prevalence of these later-evolving systems, in addition to the two types of macroscopic sense organs examined here. It is worth

mentioning, too, that our ecospace analysis focused on feeding mechanism, habitat, and motility, as is commonly done in paleontology; this focus might underweight the importance of many other biological functions such as communication, social signaling, mating, and reproduction (Bush et al. 2016), for which nervous system complexity also plays a major role but which are more difficult to study from fossil data (Hsieh and Plotnick 2020). These behaviors are nonetheless highly relevant in the evolution of information processing in animals, and they may have helped promote diversification (Bush et al. 2016).

Though Cambrian and post-Cambrian marine faunas are quite similar by our metrics, it is worth noting that terrestrial ecosystems are even more overwhelmingly dominated by brains. Only a subset of metazoans became truly terrestrial (Selden 2016), with three of the major taxa—tetrapods, panarthropods (including onychophora), and gastropods—possessing brains. Other taxa with terrestrial members, such as oligochaete annelids and platyhelminth flatworms, at least possess ganglia. No animals with decentralized nervous systems, or lacking nervous systems, made it onto land, although some colonized continental aquatic environments. The majority of animal species alive today have the cognition-associated anatomical traits we looked at in our analyses—brains, eyes, and chemoreceptive organs—due to the overwhelming richness of terrestrial insects, whose diversification has been the topic of much study (Labandeira and Sepkoski 1993; Vermeij and Grosberg 2010; Clapham et al. 2016).

With some exceptions, such as marine mammals, most well-studied directional increases in brain size have also been in terrestrial vertebrates. For instance, Cenozoic birds were larger brained than their Mesozoic counterparts according to Milner and Walsh (2009). Jerison (1970) similarly argued for a rise in relative mammalian brain size alongside an increase in overall range, though this was disputed by Radinsky (1978). A land-based lifestyle might strongly select for, if not outright require, complex active bodies with embodied cognition (as described by Trestman 2013), as many passive, immobile lifestyles are not viable for animals due to numerous differences between living

aquatically and terrestrially (Denny 1993; Vermeij and Dudley 2000; Grosberg et al. 2012; Burgess et al. 2016; Vermeij 2017). For example, marine animals have the option of either moving toward a desired resource or waiting for it to be transported to them (Bambach et al. 2007), but the inability of air currents to carry solid mass would heavily promote the former strategy and any navigational abilities it may entail. In many cases, terrestrial habitats may also be spatially more heterogeneous and complex (Grosberg et al. 2012), further favoring increased cognition (Mugan and MacIver 2020). Future research should explore the sensory, cognitive, and behavioral aspects of the water-to-land transition (e.g., Sturmbauer et al. 1996; Ord and Hsieh 2011; Ladich and Winkler 2017; Mugan and MacIver 2020).

Finally, although we examined and compared cognition in faunas using taxonomic diversity, it is worth considering a perspective from abundance. Diversity and abundance are frequently, but not always, correlated (Clapham et al. 2006), though accurate abundance data for fossil communities can often be difficult to obtain. Our view based on presence or absence of animal genera with cognition-related traits in each assemblage may miss aspects of ecological function only inferable through either absolute numbers of individuals or their relative proportions within an ecosystem (Vermeij and Herbert 2004; Jackson and Erwin 2006; Turvey and Blackburn 2011; Winfree et al. 2015; Gaston et al. 2018). Conservatively, our data tell us at least one individual animal with the given sensory or cognitive trait was present at a site and, if not transported there as bodily remains after death, had been interacting with the environment and processing information there in life (additionally, given how mobile many cognitively complex taxa are, mere presence at a fossil locality at a single point in time may not record the degree or intensity of interaction with the local environment—some long-distance pelagic migratory species may pass through the location briefly, while others may spend much greater time sensing and reacting to the habitat and its residents). Our presence-based analysis would thus not say how relatively “important” an animal was in the ecosystem in, for example,

commonness of encounter or interaction with other individuals of the same or different genera.

Well-studied and thoroughly sampled community data from the Burgess Shale and Chengjiang biotas show arthropods as a group dominating not just taxonomic diversity but also in number of individuals (Caron and Jackson 2008; Zhao et al. 2014; Nanglu et al. 2020) in Cambrian ecosystems. Even within the best-preserved and best-sampled Lagerstätten, we acknowledge that taphonomy may still influence this view, for arthropods have exoskeletons that strengthen preservation relative to soft-bodied or tiny animals that may be also quite abundant in raw numbers in marine ecosystems. In the present day, the preponderance of the world’s animal biomass is estimated to be in arthropods (though nematodes lead by numerical abundance; Bar-On et al. 2018; Van Den Hoogen et al. 2019). Bar-On et al. (2018) estimated that of the roughly 2 gigatons of carbon (Gt C) total of contemporary animal biomass, arthropods make up  $\approx 1$  Gt C, with fish at  $\approx 0.7$  Gt C and mollusks and annelids at around 0.2 Gt C. Though still a small share of all metazoan biomass, humans ( $\approx 0.06$  Gt C) and their livestock ( $\approx 0.1$  Gt C) now surpass all other non-fish vertebrates, having done so in a relatively geologically short span of time. In any case, an overwhelming share of animal biomass today is concentrated in bodies controlled with brains and sensory systems. The Cambrian information revolution fostered not only the diversification of cognitively complex organisms, but also their incredible abundance and biomass from the beginnings of the Phanerozoic up to today.

## Conclusion

Comparisons of faunal lists from Cambrian and post-Cambrian ecosystems reveal similarly high shares of animal genera with brains as well as macroscopic sensory organs. Our results show that the Cambrian radiation generated ecosystems that were very “modern” in sensory- and information-processing complexity, comparable to many ecosystems later in the Phanerozoic, even if they were less diverse and occupied less total ecospace. This is consistent with behavioral evidence, including

trace fossils, showing “modern” types of behavior existed by the Cambrian and the fact that most of the body plans and life modes requiring complex information processing (e.g., mobile predators) were present then. A major difference, however, is that the overwhelming majority of sensorially and cognitively complex animals in the Cambrian were panarthropods, whereas chordates and mollusks further diversified in later times. In both Cambrian and modern times, nervous systems permitted a variety of life modes, but the most active modes (those categorized as fully motile fast by Bambach et al. [2007]) are almost exclusively associated with brains, which first appear in the Cambrian. The increase in information-processing abilities in the Cambrian is exceptional in the history of life, equaled only perhaps during the conquest of the land. The Cambrian is likely the earliest time when a cognitive or behavioral biologist would find lots of interesting things to study.

The name “Phanerozoic” alludes to a time of macroscopic life, revealed as abundant fossils visible to the naked eye (Chadwick 1930; Schopf 1994). From the Greek for “manifest” or “visible,” the term “phaneron” had also been used in philosophy to describe all that we can observe or perceive through our faculties, the “collective total of all that is in any way or in any sense present to the mind” as defined by C. S. Peirce (Hartshorne and Weis 1931: p. 141). With the Cambrian information revolution ushering in a host of creatures that sensed and perceived the world around them, the moniker of this eon is apropos in more ways than one.

### Acknowledgments

We would like to thank D. Meyer-Dombard, F. Kenig, J. Brown, and P. Novack-Gottshall for their feedback and discussion. We would like to thank M. Patzkowsky, M. Hopkins, J. Kimmig, and two anonymous reviewers for their insightful comments on this article.

### Data Availability Statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5x69p8d43>.

### Literature Cited

- Aberhan, M., S. Nürnberg, and W. Kiessling. 2012. Vision and the diversification of Phanerozoic marine invertebrates. *Paleobiology* 38:187–204.
- Adrianov, A. V., and V. V. Malakhov. 2001. Symmetry of priapulids (Priapulida). 1. Symmetry of adults. *Journal of Morphology* 247:99–110.
- Allison, P. A. 1988. Konservat-Lagerstätten: cause and classification. *Paleobiology* 14:331–344.
- Babcock, L. E. 1993. Trilobite malformations and the fossil record of behavioral asymmetry. *Journal of Paleontology* 67:217–229.
- Bambach, R. K. 1983. Ecospace utilization and guilds in marine communities through the Phanerozoic. Pp. 719–746 in M. J. Tevesz and P. L. McCall, eds. *Biotic interactions in recent and fossil benthic communities*. Springer, Boston, Mass.
- Bambach, R. K. 1993. Seafood through time: changes in biomass, energetics, and productivity in the marine ecosystem. *Paleobiology* 19:372–397.
- Bambach, R. K., A. M. Bush, and D. H. Erwin. 2007. Autecology and the filling of ecospace: key metazoan radiations. *Palaeontology* 50:1–22.
- Bar-On, Y. M., R. Phillips, and R. Milo. 2018. The biomass distribution on Earth. *Proceedings of the National Academy of Sciences USA* 115:6506–6511.
- Barron, A. B., and C. Klein. 2016. What insects can tell us about the origins of consciousness. *Proceedings of the National Academy of Sciences USA* 113:4900–4908.
- Bartel, K. W., N. H. M. Swinburne, and S. Conway Morris. 1990. *Solnhofen: a study in Mesozoic palaeontology*. Cambridge University Press, Cambridge.
- Bassett, M. G., L. E. Popov and L. E. Holmer. 2004. The oldest-known metazoan parasite? *Journal of Paleontology* 78:1214–1216.
- Beers, J. R. 1963. The Bermuda Biological Station for Research. *American Zoologist* 3:255–257.
- Beesley, P. L., G. J. Ross, and C. J. Glasby. 2000. *Polychaetes & allies: the southern synthesis*. Fauna of Australia, Vol. 4. CSIRO Publishing, Canberra, ACT, Australia.
- Bicknell, R. D., and S. Pates. 2020. Exploring abnormal Cambrian-aged trilobites in the Smithsonian collection. *PeerJ* 8: e8453.
- Bicknell, R. D., J. R. Paterson, and M. J. Hopkins. 2019. A trilobite cluster from the Silurian Rochester Shale of New York: predation patterns and possible defensive behavior. *American Museum Novitates* 2019:1–16.
- Bottting, J. P., and J. S. Peel. 2016. Early Cambrian sponges of the Sirius Passet Biota, North Greenland. *Papers in Palaeontology* 2:463–487.
- Bottjer, D. J., and W. I. Ausich. 1986. Phanerozoic development of tiering in soft substrata suspension-feeding communities. *Paleobiology* 12:400–420.
- Bottjer, D. J., J. W. Hagadorn, and S. Q. Dornbos. 2000. The Cambrian substrate revolution. *GSA Today* 10:1–7.
- Brett, C. E., and A. Seilacher. 1991. Fossil Lagerstätten: a taphonomic consequence of event sedimentation. Pp. 283–297 in G. Einsele, W. Ricken, and A. Seilacher, eds. *Cycles and events in stratigraphy*. Springer-Verlag, Berlin.
- Buatois, L. A. 2018. *Treptichinus pedum* and the Ediacaran–Cambrian boundary: significance and caveats. *Geological Magazine* 155:174–180.
- Buatois, L. A., and M. G. Mángano. 2018. The other biodiversity record: innovations in animal-substrate interactions through geologic time. *GSA Today* 28:4–10.
- Budd, G. E., and S. Jensen. 2015. The origin of the animals and a “Savannah” hypothesis for early bilaterian evolution. *Biological Reviews* 92:446–473.
- Burgess, S. C., M. L. Baskett, R. K. Grosberg, S. G. Morgan, and R. R. Strathmann. 2016. When is dispersal for dispersal? Unifying

- marine and terrestrial perspectives. *Biological Reviews* 91:867–882.
- Bush, A. M., and R. K. Bambach. 2015. Sustained Mesozoic–Cenozoic diversification of marine Metazoa: a consistent signal from the fossil record. *Geology* 43:979–982.
- Bush, A. M., R. K. Bambach, and G. M. Daley. 2007. Changes in theoretical ecospace utilization in marine fossil assemblages between the mid-Paleozoic and late Cenozoic. *Paleobiology* 33:76–97.
- Bush, A. M., R. K. Bambach, and D. H. Erwin. 2011. Ecospace utilization during the Ediacaran radiation and the Cambrian eco-explosion. Pp. 111–133 in M. Laflamme, J. D. Schiffbauer, and S. Q. Dornbos, eds. *Quantifying the evolution of early life*. Springer, Dordrecht, Netherlands.
- Bush, A. M., G. Hunt, and R. K. Bambach. 2016. Sex and the shifting biodiversity dynamics of marine animals in deep time. *Proceedings of the National Academy of Sciences USA* 113:14073–14078.
- Butterfield, N. J. 1995. Secular distribution of Burgess-Shale-type preservation. *Lethaia* 28:1–13.
- Butterfield, N. J. 2003. Exceptional fossil preservation and the Cambrian explosion. *Integrative and Comparative Biology* 43:166–177.
- Carbone, C., and G. M. Narbonne. 2014. When life got smart: the evolution of behavioral complexity through the Ediacaran and early Cambrian of NW Canada. *Journal of Paleontology* 88:309–330.
- Caron, J. B., and D. A. Jackson. 2006. Taphonomy of the greater phyllopod bed community, Burgess Shale. *Palaios* 21:451–465.
- Caron, J. B., and D. A. Jackson. 2008. Paleontology of the greater phyllopod bed community, Burgess Shale. *Palaeogeography, Palaeoclimatology, Palaeoecology* 258:222–256.
- Caron, J. B., and J. Vannier. 2016. Waptia and the diversification of brood care in early arthropods. *Current Biology* 26:69–74.
- Cederström, P., P. Ahlberg, C. H. Nilsson, J. Ahlgren, and M. E. Eriksson. 2011. Moulting, ontogeny and sexual dimorphism in the Cambrian ptychopariid trilobite *Strenuaeva inflata* from the northern Swedish Caledonides. *Paleontology* 54:685–703.
- Chadwick, G. H. 1930. Subdivisions of geologic time. *Abstract. Geological Society of America Bulletin* 41:47–48.
- Chambers, L., and D. Brandt. 2018. Explaining gregarious behaviour in *Banffia constricta* from the Middle Cambrian Burgess Shale, British Columbia. *Lethaia* 51:120–125.
- Charbonnier, S., D. Audo, B. Caze, and V. Biot. 2014. The La Volute-sur-Rhône Lagerstätte (Middle Jurassic, France). *Comptes Rendus Palevol* 13:369–381.
- Chatterton, B. D., D. H. Collins, R. O. L. F. Ludvigsen, and P. Lane. 2003. Cryptic behaviour in trilobites: Cambrian and Silurian examples from Canada, and other related occurrences. *Special Papers in Paleontology* 70:157–174.
- Chen, J. Y. 2008. Early crest animals and the insight they provide into the evolutionary origin of craniates. *Genesis* 46:623–639.
- Chen, J. Y., D. Y. Huang, and C. W. Li. 1999. An early Cambrian craniate-like chordate. *Nature* 402:518–522.
- Chen, Z., X. Chen, C. Zhou, X. Yuan, and S. Xiao. 2018. Late Ediacaran trackways produced by bilaterian animals with paired appendages. *Science Advances* 4:eaa06691.
- Clapham, M. E., D. J. Bottjer, C. M. Powers, N. Bonuso, M. L. Fraiser, P. J. Marenco, S. Q. Dornbos, and S. B. Pruss. 2006. Assessing the ecological dominance of Phanerozoic marine invertebrates. *Palaios* 21:431–441.
- Clapham, M. E., J. A. Karr, D. B. Nicholson, A. J. Ross, and P. J. Mayhew. 2016. Ancient origin of high taxonomic richness among insects. *Proceedings of the Royal Society of London B* 283:20152476.
- Cong, P., X. Ma, X. Hou, G. D. Edgecombe, and N. J. Strausfeld. 2014. Brain structure resolves the segmental affinity of anomalocaridid appendages. *Nature* 513:538–542.
- Cong, P., X. Ma, M. Williams, D. J. Siveter, D. J. Siveter, S. E. Gabbott, D. Zhai, T. Goral, G. D. Edgecombe, and X. Hou. 2017. Host-specific infestation in early Cambrian worms. *Nature Ecology and Evolution* 1:1465–1469.
- Costello, M. J., M. Coll, R. Danovaro, P. Halpin, H. Ojaveer, and P. Miloslavich. 2010. A census of marine biodiversity knowledge, resources, and future challenges. *PLoS ONE* 5:e121110.
- Denny, M. 1993. *Air and water: the biology and physics of life's media*. Princeton University Press, Princeton, NJ.
- Droser, M. L., and D. J. Bottjer. 1989. Ordovician increase in extent and depth of bioturbation: implications for understanding early Paleozoic ecospace utilization. *Geology* 17:850–852.
- Duan, Y., J. Han, D. Fu, X. Zhang, X. Yang, T. Komiya, and D. Shu. 2014. Reproductive strategy of the bradoriid arthropod *Kunmingella douvillei* from the Lower Cambrian Chengjiang Lagerstätte, South China. *Gondwana Research* 25:983–990.
- Dukas, R., and J. M. Ratcliffe, eds. 2009. *Cognitive ecology II*. University of Chicago Press, Chicago.
- Dunne, J. A., R. J. Williams, N. D. Martinez, R. A. Wood, and D. H. Erwin. 2008. Compilation and network analyses of Cambrian food webs. *PLoS Biology* 6:e102.
- Erwin, D. H. 2020. The origin of animal body plans: a view from fossil evidence and the regulatory genome. *Development* 147:dev182899.
- Evans, S. D., J. G. Gehling, and M. L. Droser. 2019. Slime travelers: early evidence of animal mobility and feeding in an organic mat world. *Geobiology* 17:490–509.
- Evans, S. D., M. L. Droser, and D. H. Erwin. 2021. Developmental processes in Ediacara macrofossils. *Proceedings of the Royal Society of London B* 288:20203055.
- Fatka, O., and M. Szabad. 2011. Agnostids entombed under exoskeletons of paradoxid trilobites. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 259:207–215.
- Feinberg, T. E., and J. Mallatt. 2013. The evolutionary and genetic origins of consciousness in the Cambrian Period over 500 million years ago. *Frontiers in Psychology* 4:667.
- Foster, J. R., and R. R. Gaines. 2016. Taphonomy and paleoecology of the “Middle” Cambrian (Series 3) formations in Utah’s West Desert: recent finds and new data. *Resources and Geology of Utah’s West Desert*. Utah Geological Association Publication 45:291–336.
- Fu, D., X. Zhang, G. E. Budd, W. Liu, and X. Pan. 2014. Ontogeny and dimorphism of *Isoxys auritus* (Arthropoda) from the Early Cambrian Chengjiang biota, South China. *Gondwana Research* 25:975–982.
- Gabbott, S. E., C. Browning, J. N. Theron, and R. J. Whittle. 2017. The late Ordovician Soom Shale Lagerstätte: an extraordinary post-glacial fossil and sedimentary record. *Journal of the Geological Society* 174:1–9.
- Gaines, R. R. 2014. Burgess Shale-type preservation and its distribution in space and time. *Paleontological Society Paper* 20:123–146.
- García-Bellido, D. C., J. R. Paterson, G. D. Edgecombe, J. B. Jago, J. G. Gehling, and M. S. Lee. 2009. The bivalved arthropods *Isoxys* and *Tuzoia* with soft-part preservation from the lower Cambrian Emu Bay Shale Lagerstätte (Kangaroo Island, Australia). *Palaeontology* 52:1221–1241.
- Gaston, K. J., D. T. Cox, S. B. Canavelli, D. García, B. Hughes, B. Maas, D. Martínez, D. Ogada, and R. Inger. 2018. Population abundance and ecosystem service provision: the case of birds. *BioScience* 68:264–272.
- Gehling, J. G., B. N. Runnegar, and M. L. Droser. 2014. Scratch traces of large Ediacara bilaterian animals. *Journal of Paleontology* 88:284–298.
- Ginsburg, S., and E. Jablonka. 2010. The evolution of associative learning: a factor in the Cambrian explosion. *Journal of Theoretical Biology* 266:11–20.
- Grosberg, R. K., G. J. Vermeij, and P. C. Wainwright. 2012. Biodiversity in water and on land. *Current Biology* 22:R900–R903.
- Hammarlund, E. U., M. P. Smith, J. A. Rasmussen, A. T. Nielsen, D. E. Canfield, and D. A. Harper. 2019. The Sirius Passet Lagerstätte

- of North Greenland—a geochemical window on early Cambrian low-oxygen environments and ecosystems. *Geobiology* 17:12–26.
- Harper, D. A., E. U. Hammarlund, T. P. Topper, A. T. Nielsen, J. A. Rasmussen, T. Y. S. Park, and M. P. Smith. 2019. The Sirius Passet Lagerstätte of North Greenland: a remote window on the Cambrian Explosion. *Journal of the Geological Society* 176:1023–1037.
- Hartshorne, C., and P. Weiss, eds. 1931. *Collected papers of Charles Sanders Peirce*, Vol. 1. Harvard University Press, Cambridge, Mass.
- Harzsch, S., and A. Wanninger. 2010. Evolution of invertebrate nervous systems: the Chaetognatha as a case study. *Acta Zoologica* 91:35–43.
- Haug, J. T., J. B. Caron, and C. Haug. 2013. Demecology in the Cambrian: synchronized molting in arthropods from the Burgess Shale. *BMC Biology* 11:64.
- Heim, N. A., S. H. Bakshi, L. Buu, S. Chen, S. Heh, A. Jain, C. Noll, A. Patkar, N. Rizk, S. Sundararajan, I. Villante, M. L. Knope, and J. L. Payne. 2020. Respiratory medium and circulatory anatomy constrain size evolution in marine macrofauna. *Paleobiology* 46:288–303.
- Heuer, C. M., C. H. Müller, C. Todt, and R. Loesel. 2010. Comparative neuroanatomy suggests repeated reduction of neuroarchitectural complexity in Annelida. *Frontiers in Zoology* 7:1–21.
- Holmes, J. D., D. C. García-Bellido, and M. S. Y. Lee. 2018. Comparisons between Cambrian Lagerstätten assemblages using multivariate, parsimony and Bayesian methods. *Gondwana Research* 55:30–41.
- Hou, X. G., D. J. Siveter, R. J. Aldridge, and D. J. Siveter. 2008. Collective behavior in an Early Cambrian arthropod. *Science* 322:224.
- Hsieh, S., and R. E. Plotnick. 2020. The representation of animal behaviour in the fossil record. *Animal Behaviour* 169:65–80.
- Hua, H., B. R. Pratt, and L. Y. Zhang. 2003. Borings in *Cloudina* shells: complex predator-prey dynamics in the terminal Neoproterozoic. *Palaios* 18:454–459.
- Ivantsov, A., A. Nagovitsyn, and M. Zakrevskaya. 2019. Traces of locomotion of Ediacaran macroorganisms. *Geosciences* 9:395.
- Jackson, J. B., and D. H. Erwin. 2006. What can we learn about ecology and evolution from the fossil record? *Trends in Ecology and Evolution* 21:322–328.
- Jerison, H. J. 1970. Brain evolution: new light on old principles. *Science* 170:1224–1225.
- Jerison, H. J. 1973. *Evolution of the brain and intelligence*, 45<sup>th</sup> ed. Academic Press, New York.
- Kesidis, G., B. J. Slater, S. Jensen, and G. E. Budd. 2019. Caught in the act: priapulid burrowers in early Cambrian substrates. *Proceedings of the Royal Society of London B* 286:20182505.
- Kimmig, J., and B. R. Pratt. 2018. Coprolites in the Ravens Throat River Lagerstätte of northwestern Canada: implications for the middle Cambrian food web. *Palaios* 33:125–140.
- Kimmig, J., and L. C. Strotz. 2017. Coprolites in mid-Cambrian (Series 2–3) Burgess Shale-type deposits of Nevada and Utah and their ecological implications. *Bulletin of Geosciences* 92:297–309.
- Knope, M. L., N. A. Heim, L. O. Frishkoff, and J. L. Payne. 2015. Limited role of functional differentiation in early diversification of animals. *Nature Communications* 6:1–6.
- Labandeira, C. C., and J. J. Sepkoski. 1993. Insect diversity in the fossil record. *Science* 261:310–315.
- Ladich, F., and H. Winkler. 2017. Acoustic communication in terrestrial and aquatic vertebrates. *Journal of Experimental Biology* 220:2306–2317.
- Li, Y., M. Williams, T. H. Harvey, F. Wei, Y. Zhao, J. Guo, S. Gabbott, T. Fletcher, X. Hou, and P. Cong. 2020. Symbiotic fouling of *Vetulicola*, an early Cambrian nektonic animal. *Communications Biology* 3:1–9.
- Ma, X., X. Hou, G. D. Edgecombe, and N. J. Strausfeld. 2012. Complex brain and optic lobes in an early Cambrian arthropod. *Nature* 490:258–261.
- Mángano, M. G., and L. A. Buatois. 2020. The rise and early evolution of animals: where do we stand from a trace-fossil perspective? *Interface Focus* 10:20190103.
- Manojlovic, M., and M. E. Clapham. 2021. The role of bioturbation-driven substrate disturbance in the Mesozoic brachiopod decline. *Paleobiology* 47:86–100.
- Marshall, C. R. 2006. Explaining the Cambrian “explosion” of animals. *Annual Review of Earth and Planetary Sciences* 34:355–384.
- Martill, D. M., and J. D. Hudson. 1991. Fossils of the Oxford clay. *Palaeontological Association*.
- Meinertzhagen, I. A. 2010. The organisation of invertebrate brains: cells, synapses and circuits. *Acta Zoologica* 91:64–71.
- Milner, A. C., and S. A. Walsh. 2009. Avian brain evolution: new data from Palaeogene birds (Lower Eocene) from England. *Zoological Journal of the Linnean Society* 155:198–219.
- Morris, S. C., and J. B. Caron. 2012. *Pikaia gracilens* Walcott, a stem-group chordate from the Middle Cambrian of British Columbia. *Biological Reviews* 87:480–512.
- Mugan, U., and M. A. MacIver. 2020. Spatial planning with long visual range benefits escape from visual predators in complex naturalistic environments. *Nature Communications* 11:1–14.
- Nanglu, K., and J. B. Caron. 2018. A new Burgess Shale polychaete and the origin of the annelid head revisited. *Current Biology* 28:319–326.
- Nanglu, K., and J. B. Caron. 2021. Symbiosis in the Cambrian: enteropneust tubes from the Burgess Shale co-inhabited by commensal polychaetes. *Proceedings of the Royal Society of London B* 288:20210061.
- Nanglu, K., J. B. Caron, and C. B. Cameron. 2015. Using experimental decay of modern forms to reconstruct the early evolution and morphology of fossil enteropneusts. *Paleobiology* 41:460–478.
- Nanglu, K., J. B. Caron, and R. R. Gaines. 2020. The Burgess Shale paleocommunity with new insights from Marble Canyon, British Columbia. *Paleobiology* 46:58–81.
- Nickel, M. 2010. Evolutionary emergence of synaptic nervous systems: what can we learn from the non-synaptic, nerveless Porifera? *Invertebrate Biology* 129:1–16.
- Northcutt, R. G. 2002. Understanding vertebrate brain evolution. *Integrative and Comparative Biology* 42:743–756.
- Northcutt, R. G. 2012. Evolution of centralized nervous systems: two schools of evolutionary thought. *Proceedings of the National Academy of Sciences USA* 109(Suppl. 1):10626–10633.
- Ord, T. J., and S. T. Hsieh. 2011. A highly social, land-dwelling fish defends territories in a constantly fluctuating environment. *Ethology* 117:918–927.
- Orrhage, L., and M. C. Müller. 2005. Morphology of the nervous system of Polychaeta (Annelida). *Hydrobiologia* 535:79–111.
- Parker, A. 2003. *In the blink of an eye: how vision sparked the big bang of evolution*. Basic Books, New York.
- Parker, A. R. 1998. Colour in Burgess Shale animals and the effect of light on evolution in the Cambrian. *Proceedings of the Royal Society of London B* 265:967–972.
- Parry, L., and J. B. Caron. 2019. *Canadia spinosa* and the early evolution of the annelid nervous system. *Science Advances* 5:eaa5858.
- Paterson, J. R., D. C. García-Bellido, M. S. Lee, G. A. Brock, J. B. Jago, and G. D. Edgecombe. 2011. Acute vision in the giant Cambrian predator *Anomalocaris* and the origin of compound eyes. *Nature* 480:237–240.
- Paterson, J. R., G. D. Edgecombe, and D. C. García-Bellido. 2020. Disparate compound eyes of Cambrian radiodonts reveal their developmental growth mode and diverse visual ecology. *Science Advances* 6:eabc6721.
- Pates, S., and R. D. Bicknell. 2019. Elongated thoracic spines as potential predatory deterrents in olenelline trilobites from the lower Cambrian of Nevada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 516:295–306.

- Paulin, M. G., and J. Cahill-Lane. 2021. Events in early nervous system evolution. *Topics in Cognitive Science* 13:25–44.
- Pickerrill, R. K., and D. Blissett. 1999. A predatory *Rusophycus* burrow from the Cambrian of southern New Brunswick, eastern Canada. *Atlantic Geology* 35:179–183.
- Plotnick, R. E., S. Q. Dornbos, and J. Chen. 2010. Information landscapes and sensory ecology of the Cambrian radiation. *Paleobiology* 36:303–317.
- Radinsky, L. 1978. Evolution of brain size in carnivores and ungulates. *American Naturalist* 112:815–831.
- Rayner, D. 2009. London clay fossils of Kent and Essex. Medway Fossil and Mineral Society, Rochester, U.K.
- Rouse, G., and F. Pleijel. 2001. *Polychaetes*. Oxford University Press, Oxford.
- Russell, D. A. 1981. Speculations on the evolution of intelligence in multicellular organisms. NASA Conference Publication 2156:259.
- Russell, D. A. 1983. Exponential evolution: implications for intelligent extraterrestrial life. *Advances in Space Research* 3:95–103.
- Saleh, F., J. B. Antcliffe, B. Lefebvre, B. Pittet, L. Laibl, F. P. Peris, L. Lustrì, P. Gueriau, and A. C. Daley. 2020. Taphonomic bias in exceptionally preserved biotas. *Earth and Planetary Science Letters* 529:115873.
- Schoenemann, B., and E. N. Clarkson. 2013. Discovery of some 400 million year-old sensory structures in the compound eyes of trilobites. *Scientific Reports* 3:1429.
- Schoenemann, B., and E. N. Clarkson. 2017. Vision in fossilised eyes. *Transactions of the Royal Society of Edinburgh (Earth and Environmental Science)* 106:209–220.
- Schopf, J. W. 1994. The early evolution of life: solution to Darwin's dilemma. *Trends in Ecology and Evolution* 9:375–377.
- Seilacher, A., and F. Pflüger. 1994. From biomas to benthic agriculture: a biohistoric revolution. Pp. 97–105 in W. Krumbein, D. Paterson, and L. Stal, eds. *Biostabilisation of sediments. Bibliotheks und Informationssystem der Carl von Ossietzky Universität Oldenburg (BIS)*, Oldenburg, Germany.
- Selden, P. A. 2016. Land animals, origins of. Pp. 288–295 in R. M. Kliman, ed. *Encyclopedia of evolutionary biology*. Elsevier, Amsterdam.
- Selly, T., J. W. Huntley, K. L. Shelton, and J. D. Schiffbauer. 2016. Ichnofossil record of selective predation by Cambrian trilobites. *Palaeogeography, Palaeoclimatology, Palaeoecology* 444:28–38.
- Sepkoski, J. J. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7:36–53.
- Sepkoski, J. J. 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10:246–267.
- Servais, T., and D. A. Harper. 2018. The great Ordovician biodiversification event (GOBE): definition, concept and duration. *Lethaia* 51:151–164.
- Shen, C., B. R. Pratt, and X. G. Zhang. 2014. Phosphatized coprolites from the middle Cambrian (Stage 5) Duyun fauna of China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 410:104–112.
- Shimeld, S. M., and P. W. Holland. 2000. Vertebrate innovations. *Proceedings of the National Academy of Sciences USA* 97:4449–4452.
- Shu, D. G., S. C. Morris, J. Han, Z. F. Zhang, K. Yasui, P. Janvier, L. Chen, X. L. Zhang, J. N. Liu, Y. Li, and H. Q. Liu. 2003. Head and backbone of the Early Cambrian vertebrate *Haikouichthys*. *Nature* 421:526–529.
- Smith, F. A., J. L. Payne, N. A. Heim, M. A. Balk, S. Finnegan, M. Kowalewski, S. K. Lyons, C. R. McClain, D. W. McShea, P. M. Novack-Gottshall, and P. S. Anich. 2016. Body size evolution across the Geozoic. *Annual Review of Earth and Planetary Sciences* 44:523–553.
- Smith, M. R. 2013. Nectocaridid ecology, diversity, and affinity: early origin of a cephalopod-like body plan. *Paleobiology* 39:297–321.
- Sterrer, W., and C. Schoepfer-Sterrer. 1986. Marine fauna and flora of Bermuda: a systematic guide to the identification of marine organisms. Wiley, New York.
- Strausfeld, N. J. 2011. Some observations on the sensory organization of the crustacean form *Waptia fieldensis* Walcott. *Palaeontographica Canadiana* 31:157–168.
- Strausfeld, N. J. 2015. Palaeontology: clearing the heads of Cambrian arthropods. *Current Biology* 25:R616–R618.
- Strausfeld, N. J. 2016. *Waptia* revisited: intimations of behaviors. *Arthropod Structure and Development* 45:173–184.
- Sturmbauer, C., Levinton, J. S., and J. Christy. 1996. Molecular phylogeny analysis of fiddler crabs: test of the hypothesis of increasing behavioral complexity in evolution. *Proceedings of the National Academy of Sciences USA* 93:10855–10857.
- Südkamp, W. 2017. *Leben im Devon—Bestimmungsbuch Hunsrück-schieferfossilien/Life in the Devonian—identification book Hunsrück Slate fossils*. Verlag Dr. Friedrich Pfeil, Munich.
- Sutcliffe, O. E., D. E. Briggs, and C. Bartels. 1999. Ichnological evidence for the environmental setting of the Fossil-Lagerstätten in the Devonian Hunsrück Slate, Germany. *Geology* 27:275–278.
- Tanaka, G., X. Hou, X. Ma, G. D. Edgecombe, and N. J. Strausfeld. 2013. Chelicerate neural ground pattern in a Cambrian great appendage arthropod. *Nature* 502:364–367.
- Topper, T. P., L. E. Holmer, and J. B. Caron. 2014. Brachiopods hitching a ride: an early case of commensalism in the middle Cambrian Burgess Shale. *Scientific Reports* 4:1–5.
- Topper, T. P., L. C. Strotz, L. E. Holmer, Z. Zhang, N. N. Tait, and J. B. Caron. 2015. Competition and mimicry: the curious case of chaetae in brachiopods from the middle Cambrian Burgess Shale. *BMC Evolutionary Biology* 15:42.
- Trestman, M. 2013. The Cambrian explosion and the origins of embodied cognition. *Biological Theory* 8:80–92.
- Turvey, S. T., and T. M. Blackburn. 2011. Determinants of species abundance in the Quaternary vertebrate fossil record. *Paleobiology* 37:537–546.
- Valentine, J. W. 2002. Prelude to the Cambrian explosion. *Annual Review of Earth and Planetary Sciences* 30:285–306.
- Van Den Hoogen, J., S. Geisen, D. Routh, H. Ferris, W. Traunspurger, D. A. Wardle, R. G. De Goede, B. J. Adams, W. Ahmad, W. S. Andriuzzi, and R. D. Bardgett. 2019. Soil nematode abundance and functional group composition at a global scale. *Nature* 572:194–198.
- Vannier, J., 2012. Gut contents as direct indicators for trophic relationships in the Cambrian marine ecosystem. *PLoS ONE* 7: e52200.
- Vannier, J., Steiner, M., Renvoisé, E., Hu, S.X., and J. P. Casanova. 2007. Early Cambrian origin of modern food webs: evidence from predator arrow worms. *Proceedings of the Royal Society of London B* 274:627–633.
- Vannier, J., D. C. García-Bellido, S. X. Hu, and A. L. Chen. 2009. Arthropod visual predators in the early pelagic ecosystem: evidence from the Burgess Shale and Chengjiang biotas. *Proceedings of the Royal Society of London B* 276:2567–2574.
- Vannier, J., I. Calandra, C. Gaillard, and A. Żylińska. 2010. Priapulid worms: pioneer horizontal burrowers at the Precambrian–Cambrian boundary. *Geology* 38:711–714.
- Vannier, J., C. Aria, R. S. Taylor, and J. B. Caron. 2018. *Waptia fieldensis* Walcott, a mandibulate arthropod from the middle Cambrian Burgess Shale. *Royal Society Open Science* 5:172206.
- Van Roy, P., D. E. Briggs, and R. R. Gaines. 2015. The Fezouata fossils of Morocco; an extraordinary record of marine life in the Early Ordovician. *Journal of the Geological Society* 172:541–549.
- Vermeij, G. J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* 3:245–258.
- Vermeij, G. J. 1993. *Evolution and escalation: an ecological history of life*. Princeton University Press, Princeton, NJ.

- Vermeij, G. J. 2017. How the land became the locus of major evolutionary innovations. *Current Biology* 27:3178–3182.
- Vermeij, G. J., and R. Dudley. 2000. Why are there so few evolutionary transitions between aquatic and terrestrial ecosystems? *Biological Journal of the Linnean Society* 70:541–554.
- Vermeij, G. J., and R. K. Grosberg. 2010. The great divergence: when did diversity on land exceed that in the sea? *Integrative and Comparative Biology* 50:675–682.
- Vermeij, G. J., and G. S. Herbert. 2004. Measuring relative abundance in fossil and living assemblages. *Paleobiology* 30:1–4.
- Vinn, O. 2017. Early symbiotic interactions in the Cambrian. *Palaios* 32:231–237.
- Winfree, R., J. W. Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters* 18:626–635.
- Wittry, J. 2012. The Mazon Creek fossil fauna. ESCONI/Northeastern Illinois University, Chicago.
- Wood, R. 1999. Reef evolution. Oxford University Press on Demand.
- Wu, W., M. Zhu, and M. Steiner. 2014. Composition and tiering of the Cambrian sponge communities. *Palaeogeography, Palaeoclimatology, Palaeoecology* 398:86–96.
- Xian-guang, H., D. J. Siveter, R. J. Aldridge, and D. J. Siveter. 2009. A new arthropod in chain-like associations from the Chengjiang Lagerstätte (Lower Cambrian), Yunnan, China. *Palaeontology* 52:951–961.
- Yang, X. Y., J. Vannier, J. Yang, D. Wang, and X. G. Zhang. 2021. Priapulid worms from the Cambrian of China shed light on reproduction in early animals. *Geoscience Frontiers* 12:101234.
- Zhang, X. G. 1987. Moulting stages and dimorphism of Early Cambrian bradoriids from Xichuan, Henan, China. *Alcheringa* 11:1–19.
- Zhang, Z., L. C. Strotz, T. P. Topper, F. Chen, Y. Chen, Y. Liang, Z. Zhang, C. B. Skovsted, and G. A. Brock. 2020. An encrusting kleptoparasite-host interaction from the early Cambrian. *Nature Communications* 11:1–7.
- Zhao, F., D. J. Bottjer, S. Hu, Z. Yin, and M. Zhu. 2013. Complexity and diversity of eyes in Early Cambrian ecosystems. *Scientific Reports*, 3:2751.
- Zhao, F., J. B. Caron, D. J. Bottjer, S. Hu, Z. Yin, and M. Zhu. 2014. Diversity and species abundance patterns of the early Cambrian (Series 2, Stage 3) Chengjiang Biota from China. *Paleobiology* 40:50–69.
- Zhu, M. Y., J. Vannier, H. V. Iten, and Y. L. Zhao. 2004. Direct evidence for predation on trilobites in the Cambrian. *Proceedings of the Royal Society of London B* 271(Suppl. 5):S277–S280.