

Oxygen, ecology, and the Cambrian radiation of animals

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The Proterozoic-Cambrian transition records the appearance of essentially all animal body plans (phyla), yet to date no single hypothesis adequately explains both the timing of the event and the evident increase in diversity and disparity. Ecological triggers focused on escalatory predator–prey “arms races” can explain the evolutionary pattern but not its timing, whereas environmental triggers, particularly ocean/atmosphere oxygenation, do the reverse. Using modern oxygen minimum zones as an analog for Proterozoic oceans, we explore the effect of low oxygen levels on the feeding ecology of polychaetes, the dominant macrofaunal animals in deep-sea sediments. Here we show that low oxygen is clearly linked to low proportions of carnivores in a community and low diversity of carnivorous taxa, whereas higher oxygen levels support more complex food webs. The recognition of a physiological control on carnivory therefore links environmental triggers and ecological drivers, providing an integrated explanation for both the pattern and timing of Cambrian animal radiation.

evolution | hypoxia | Ediacaran | Metazoa

Cambrian fossils chronicle the appearance of essentially all high-level animal body plans, as measured by cumulative first appearances of metazoan phyla and classes, in a geologically brief interval between ~540 and 500 million years ago (1, 2). Hypotheses to explain this event have commonly focused on either external controls, such as increasing oxygenation of the atmosphere–ocean system (1, 3–5), or internal controls based on an evolutionary, ecological, or genomic breakthrough (2, 6–11). Recently, hypotheses in the latter category have emphasized the importance of macropredation in facilitating observed increases in diversity and disparity across the Proterozoic-Cambrian transition (6–10).

External and internal controls have distinct attractions as triggers for Cambrian radiation. External controls relating to environmental oxygenation can explain the timing of the radiation—in other words, why animals radiated so dramatically beginning ~540 Ma, and not earlier or later. Indeed, the appearance of large, complex animals in the fossil record seems to follow directly on the heels of an Ediacaran increase and stabilization of marine oxygen levels as inferred from a number of different proxy records (12, 13). Such an environmental shift could remove a barrier to animal evolution, but aside from direct links to maximum permissible body size (14), it lacks an explicit mechanism to generate diversity (new species) and disparity (new body plans). There is no theoretical reason why ocean redox change should generate the evolutionary novelties—specifically the fundamentally new bauplans—seen in the Cambrian fossil record (15).

In contrast, ecological hypotheses focused on predation contain a clear driving mechanism for morphological innovation, namely selection pressures in evolving food webs. They can also explain the origin and maintenance of high-level body plan disparity through the principle of frustration: organisms optimally suited to one task will be less well suited for another, leading to a roughening of the fitness landscape and isolation of distinct fitness peaks (16). Consistent with this hypothesis, the origin of

carnivory itself appears to be temporally correlated with the Proterozoic-Cambrian transition (Fig. 1), a prerequisite if predator–prey “arms races” are to be viewed as the driving forces behind morphological innovation. In this discussion, we distinguish carnivory as mobile animal–animal interactions, as opposed to predation, which more broadly refers to one organism consuming another and may be as ancient as Eukarya (17). The oldest paleontological evidence for carnivory comes from circular perforations interpreted as drill holes in the lightly biomineralized metazoan fossil *Cloudina* from upper Ediacaran rocks in China (18). Strong evidence for carnivory can further be found in chaetognath fossils—voracious predators in the modern ocean—including the widespread early Cambrian skeletal fossil *Protohertzina*, interpreted as chaetognath grasping spines (19), and early Cambrian body fossils (20). Fossil aggregates and preserved gut contents in Cambrian Lagerstätten (e.g., hyolith shells in priapulid guts) provide additional fossil evidence for carnivory in early Cambrian oceans (21).

Support for the origin of carnivory near the Proterozoic-Cambrian boundary also comes from the qualitative mapping of feeding strategies onto a time-calibrated metazoan phylogeny (2). This suggests that the last common ancestor of bilaterians and the last common ancestors of the bilaterian superclades Deuterostomia, Ecdysozoa, and Lophotrochozoa were unlikely to have been carnivorous. Evolution of the carnivorous habit cannot be constrained with confidence on the tree until the origin of crown group Nemertea (Fig. 1). Priapulids are another clade that likely evolved carnivory around the Proterozoic-Cambrian transition, although the timing can only currently be constrained between their divergence from kinorhynchs and the appearance of early Cambrian predatory forms (21), as the Priapulida crown group is undated and it is unclear whether the small nonpredatory forms at the base of this clade in morphological cladistics trees (22) represent the primitive form or are derived from a larger, potentially carnivorous ancestor. Molecular clock ages for nodes constraining the evolution of carnivory (2, 23) clearly suggest that bilaterians originated long before carnivory evolved within the clade around the Proterozoic-Cambrian transition (Fig. 1). It is worth noting that the derived nature of carnivory and the logic of phylogenetic systematics requires such a conclusion at some level regardless of the accuracy of molecular clock ages. A carnivory-based ecological hypothesis, then, can explain the pattern of morphological diversification seen in the Cambrian fossil record but does not directly address its timing.

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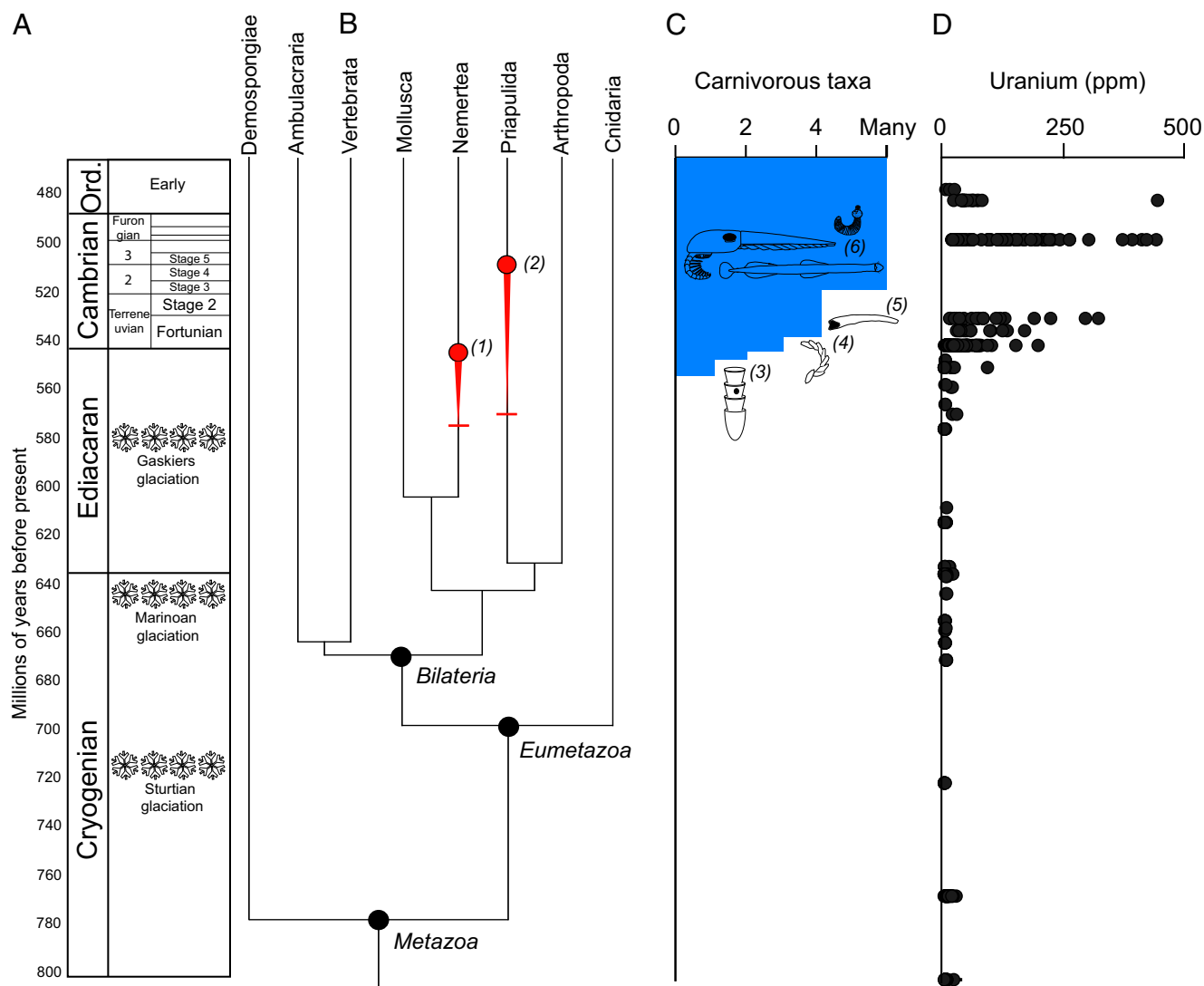


Fig. 1. The temporal origins of carnivory in animals. (A) Geological time scale for the Cryogenian–Ordovician (Ord.). (B and C) Origins of carnivorous metazoans as inferred from the molecular (2, 23) and fossil records. In B, red horizontal whiskers represent maximum estimates for the evolution of carnivory in nemerteans and priapulids as constrained by molecular clock ages for their divergence from noncarnivorous sister groups. Red circles represent minimum ages for carnivory as constrained by the nemertean crown group (1), as all extant nemerteans are carnivores, and early Cambrian priapulid fossils (2) with gut contents indicating a carnivorous habit. Carnivory evolved between these minimum and maximum age estimates. In C, fossil evidence for carnivory around the Precambrian–Cambrian transition includes apparent drill holes in the fossil *Cloudina* (3); the trace fossil *Treptichnus pedom*, if it represents the burrowing activities of carnivorous priapulids (4) (7); and the widespread early Cambrian small shelly fossil *Protohertzina*, interpreted as grasping spines of chaetognaths (19) (5). By series 2 and 3 of the Cambrian, fossil Lagerstätten record numerous carnivores including a variety of arthropods, priapulids with hyolith gut contents, and chaetognath body fossils (6) (reviewed by ref. 21). (D) The origin of carnivory coincides with a major increase in the concentration of uranium and other redox-sensitive trace elements in organic-rich, fine-grained sedimentary rocks (data replotted from ref. 48). Higher values indicate higher seawater concentrations of U and more widespread oxygenation. Other redox proxies for this interval, including patterns similar to uranium for molybdenum and vanadium, are reviewed by refs. 12 and 13.

Based on a global study of feeding strategies in modern oxygen minimum zones (OMZs), we argue here that environmental and ecological hypotheses for Cambrian animal diversification are not decoupled, but can be linked through the lens of physiological constraint. Modern OMZs impinge on more than 10^6 km² of seafloor (as determined at the <0.5 mL/L or 22 μM O₂ level) (24) and can serve as an analog for ancient low-oxygen oceans (4, 25). In modern OMZs, the low-oxygen conditions are important in structuring the diversity and abundance of benthic communities (26–29). Some studies have considered how changing oxygen levels affect feeding strategies in individual basins, especially among polychaetes, but unlike studies of diversity (27), a global synthesis analysis of oxygen effects on carnivory has not been conducted.

Oxygen and Carnivory in Modern OMZs

We assembled a data set comprising polychaete occurrences in low-oxygen (<2 mL/L O₂; <89 μM) settings from below 150 m water depth. Water depth was constrained to be essentially beneath storm wave base, thus removing the effects of atmospheric mixing, which cause fluctuating oxygen levels not necessarily represented during sampling. Only studies using a sieve size ≤500 μm were used (30). Polychaetes were chosen as the study taxon for five reasons. First, they are the dominant macrofaunal taxon in deep-sea sediments and are especially abundant at low bottom-water oxygen concentrations, constituting up to 90% of the total fauna by abundance (26). Second, they exhibit a diversity of feeding strategies, including surface- and subsurface-deposit feeding, detritivory, filter feeding, carnivory, and even

chemosymbiosis. Third, their feeding biology is relatively well understood (31), and although the feeding of most deep-sea polychaetes has not been observed *in vivo*, it is possible to code feeding strategies with reference to shallow water relatives. Fourth, polychaetes are more tolerant of low-oxygen levels than most other bilaterians, including arthropods and vertebrates (26, 32) and so constitute a conservative choice for our study. Finally, the use of a single group ensures that all taxa will have broadly similar physiologies and body plans, and observed trends will not be the result of ecological replacement by a different taxon with a fundamentally different bauplan. Similar correlations between oxygen and feeding ecology were found for the entire fauna in a single basin investigation of the western Indian OMZ (33), suggesting that the results extend beyond polychaetes and are unlikely to be specific to this clade.

A total of 10 published studies were identified that met the oxygen, depth, and sieve size requirements outlined above, resulting in a full data set that includes 962 polychaete species occurrences from 68 stations worldwide (Table 1 and Dataset S1). In addition to the 10 studies analyzed quantitatively for the relationship between oxygen and carnivory, a new data set from the Bay of Bengal, which contains additional very low-oxygen sites, was analyzed qualitatively for the presence-absence of carnivores. All species occurrences were coded for their likely feeding mode based on the literature, incorporating both classical observations and gut content analyses, as well as new insights from tracer studies, stable isotopes, and fatty acid analysis (see *SI Materials and Methods* for full coding details). In some cases, there was uncertainty in coding due to either contradictory information in the literature or low taxonomic resolution in faunal lists for higher taxa that are known to feed heterogeneously. In these cases, as well as for omnivorous taxa, we followed the logic of ref. 34 in counting these taxa as one-half carnivore for the purposes of calculating the number of carnivorous individuals in a fauna and the number of carnivorous taxa. To test the effect of this coding strategy, sensitivity analyses were conducted wherein all uncertain and omnivorous taxa were coded as either entirely carnivorous or noncarnivorous.

The percentage of carnivorous individuals in an assemblage and number of carnivorous taxa in an assemblage were binned for four different oxygen levels: suboxia (0–0.2 mL/L O₂, or 0–9 μM; 26 stations), severe hypoxia (0.2–0.5 mL/L O₂, or 9–22 μM; 13 stations), moderate hypoxia (0.5–1.0 mL/L O₂, or 22–45 μM; 9 stations), and mild hypoxia (1.0–2.0 mL/L O₂, or 45–89 μM; 20 stations). Binning of stations was guided by table 1 of ref. 35, which describes various O₂ thresholds currently used in the low-O₂ literature. We acknowledge that there are several different definitions for these thresholds, and, in particular, any definition

of suboxia based on dissolved O₂ concentration will encompass a variety of biogeochemical environments including many dominated by purely aerobic metabolisms (36) (see *SI Materials and Methods* for binning details).

Presence-absence data for carnivores across the data set illustrate a clear relationship to oxygen. Some carnivores can survive at low oxygen levels—but carnivores are only absent from an assemblage when oxygen is <0.34 mL/L (~15 μM; Fig. 2A). A similar pattern was seen in the Bay of Bengal (Table S1). The other investigated metrics for carnivory also show a relationship with oxygen level (Fig. 2B and C). To test for significant differences in percent of carnivorous individuals and number of carnivorous taxa among oxygen levels, the data were log-transformed and compared using ANOVA. Post hoc Tukey-Kramer tests ($\alpha = 0.05$) were used to further explore significant differences among oxygen levels. Percent carnivorous individuals (Fig. 2B) increased dramatically between suboxic and hypoxic environments ($F_{3,64} = 14.25$; $P < 0.0001$). Indeed, half the suboxic stations had no carnivores at all. The striking relationship between oxygen and feeding ecology is further shown by comparing the number of carnivorous taxa present, a measure of food web complexity, against oxygen (Fig. 2C). The number of carnivorous polychaete taxa in suboxic conditions was significantly lower than at higher oxygen settings ($F_{3,64} = 20.4$; $P < 0.0001$). These results are robust with respect to assumptions regarding feeding mode uncertainty (Tables S2 and S3). Although these analyses focus on oxygen, we recognize that other environmental parameters and physiological stressors may be important in shaping the biology of modern OMZs (26). Many potentially important variables, such as lower pH or high ammonium and sulfide levels in the sediment, can be ameliorated physiologically, although this typically requires an energetic expenditure (37). Because aerobic respiration is the means by which animals regenerate the majority of their ATP, the ability to cope with these stressors thus largely remains linked to oxygen availability.

The global analysis of feeding strategies demonstrates a strong relationship between oxygen and the presence-absence of carnivores, the percentage of carnivores in an assemblage, and food web complexity as measured by species diversity of carnivores. The precise reasons why carnivores are excluded from low-oxygen environments are not fully understood, but several (non-exclusive) possibilities can be considered. The ability to be a successful carnivore will relate fundamentally to the energy expended while catching and digesting prey vs. the total energy gained. In general, macrofaunal abundances remain steady, or even increase (28), with respect to declining oxygen until it reaches very low levels, below which organismal densities drop precipitously (26). The lack of predators at the very lowest

Table 1. Analyzed studies

Study	Reference	Margin	Number of stations	Oxygen range (mL/L)
Díaz-Casteñada and Harris, 2004	49	Baja California, Mexico	6	1.0–1.4
Vetter and Dayton, 1998	50	Southern California	5	0.45–1.39
Levin et al., 2010; this study	51	California and Oregon	9	0.22–0.66
Levin et al., 2000	52	Oman	5	0.13–0.52
Hughes et al., 2009	53	Pakistan	8	0.1–1.78
Gallardo et al., 2004	54	Central Chile	2	0.13–0.52
Palma et al., 2005	55	Chile	11	0.06–1.93
Levin et al., 2009	56	Pakistan	16	0.117–0.2
Levin et al., 1991	57	Volcano 7, off Mexico	3	0.09–0.81
Ingole et al., 2010	27	Western Indian	3	0.08–1.35
A. Raman, this study		Bay of Bengal	38	0.01–1.19

Number of stations refers to the stations within the specified depth and O₂ range investigated here and not the total number of stations in a given study. Oxygen concentrations reported as in the published studies (mL/L O₂); for reference, 0.2 mL/L ~ 9 μmol/kg ~ 0.29 mg/L ~ 9 matm (also see ref. 35).

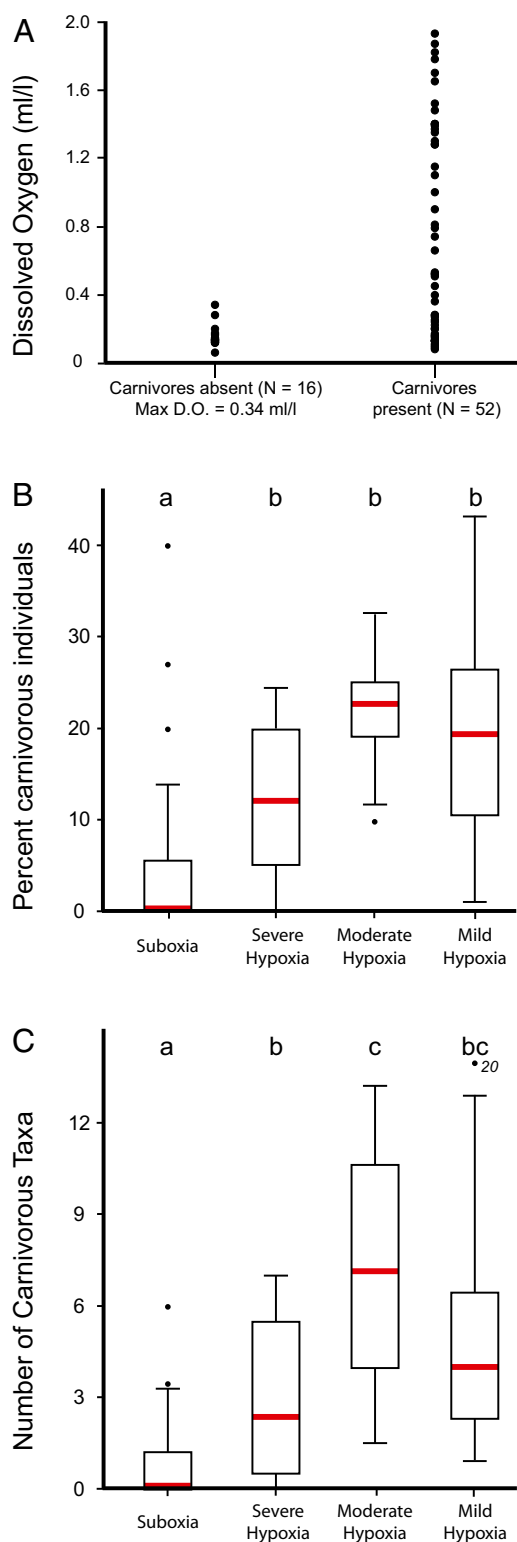


Fig. 2. Relationship between oxygen and carnivory in modern oxygen minimum zones. (A) Bottom-water oxygen concentrations at stations with carnivores present and absent. D.O., dissolved oxygen. (B and C) Standard box-and-whisker plots of percent carnivorous individuals (B) and number of carnivorous taxa (C) against four oxygen bins: suboxia (0–0.2 mL/L O₂, or 0–9 μM; 26 stations), severe hypoxia (0.2–0.5 mL/L O₂, or 9–22 μM; 13 stations), moderate hypoxia (0.5–1.0 mL/L O₂, or 22–45 μM; 9 stations), and mild hypoxia (1.0–2.0 mL/L O₂, or 45–89 μM; 20 stations). For box plots, the box encompasses the first and third quartiles, thick bar depicts the median, and whiskers depict true minimum and maximum values except where outliers

oxygen stations may therefore simply be a function of extremely low prey densities. This possibility is countered by the lack of polychaete carnivores feeding on abundant meiofaunal nematodes that characterize OMZ cores (26). A physiological cause is likely required.

As there is a direct relationship between oxygen and maximum permissible body size (14), a second possibility is the higher oxygen requirement of larger body size. Given that many predators are larger than their prey, decreasing size with lower oxygen levels (26, 38) may place a physiological limit on the ability of a carnivore to be larger than its prey. We suggest that the most likely reason for the dearth of carnivores in modern low-oxygen benthic environments is an inability to pay off the accumulated oxygen debt of a carnivorous lifestyle. Active carnivory, specifically capturing and subduing prey, is energetically costly (equals high oxygen demand) compared with either deposit or suspension feeding. In deposit and suspension feeding the mechanical costs of feeding are low and constant relative to total metabolism (39, 40). The metabolic cost of digestion (41) may also be important for low-oxygen settings. Filter and deposit feeders can maintain a continuous food input and thereby a more or less constant reduced carbon load in their gut. In contrast, many carnivores (especially those that engulf prey whole) are episodically faced with very large reduced carbon loads. Indeed, this observation forms the foundation of feeding mode inference from gut content analysis (31): deposit feeders and detritivores almost continuously have guts filled with sedimentary particles and detritus, whereas intermittently feeding carnivores are usually characterized by empty guts. Together, active and muscular predation followed by digestion of a relatively large food item results in episodically high oxygen demand. The pelagic realm of modern OMZs is characterized by a diversity of carnivores that, in the cores of OMZs, usually migrate to more oxygenated water to pay off this oxygen debt (42). Interestingly, however, some permanently pelagic OMZ residents such as the vampire squid have adapted to low-oxygen levels by losing the carnivorous feeding habit that is primitive for cephalopods and becoming detritivores (43). The inability to pay off an oxygen debt in the chronically low-oxygen benthos, where organisms are unable to migrate to higher-O₂ waters, represents the most likely explanation for the observation that polychaete carnivore species diversity and percentage of the total fauna correlate with oxygen level.

Conclusions

The observation that oxygen and feeding ecology are linked by physiology in the modern ocean suggests that ecological and environmental triggers for the Cambrian radiation can be integrated in a new causal hypothesis for Cambrian animal diversification. Modern OMZs indicate that low Proterozoic oxygen levels could have supported diploblastic animals and small, thin bilaterians (25), but also that any such animals in Neoproterozoic oceans would have been constrained to small sizes and to lifestyles and feeding modes that incur little oxygen debt. This would have limited both their fossilization potential and their capacity to drive evolutionary arms races via carnivory. Rising oxygen levels would have allowed larger body sizes, but more importantly from a macroevolutionary standpoint, the first active, muscular carnivores. The establishment of stable redox conditions (44) (even if pO₂ remained relatively low) may have been as important as the absolute magnitude of change itself, as unpredictable redox conditions would be deleterious

(dots) greater than 1.5 times the interquartile range were identified. Means with the same lowercase letter at the top of the graph are not significantly different based on Tukey HSD test ($\alpha = 0.05$). Outlier in mild hypoxia bin in C not to scale.

to carnivores with the fluctuating oxygen demands described above. Escalatory arms races driven by these newly evolved carnivores could then explain the relatively rapid expansion of metazoan diversity and disparity near the beginning of the Cambrian Period.

An Ediacaran transition in the availability of oxygen, allowing widespread carnivory, can thus explain both the timing and recorded biological pattern of Cambrian animal diversification. Specifically, the key physiological threshold in regard to the Cambrian radiation was likely not one of body size alone but rather ecological feeding strategy. Given evolving physiologies through time, the specific oxygen levels at which ecological effects are seen in the modern may not directly relate to Proterozoic oceans. However, because carnivory in polychaetes is limited at low oxygen levels despite their being among the most low oxygen-tolerant taxa in the modern ocean (26, 32), with high-affinity respiratory pigments and good acid-base regulation—and 500 million years of natural selection doubtfully made carnivores less fit—it seems inescapable that low Proterozoic oxygen levels would have limited early animal food webs. Other factors besides carnivory and oxygen may have been important, but many of them are related to carnivore evolution itself (e.g., the evolution of sensory apparatus and vision) (11). This focus does not obviate a role for developmental genetics, but because most gene families that govern bilaterian development originated well before Cambrian body

plan diversification (2, 45), the prime role of development was in assembling these preexisting genes into coherent networks to build body plans suited to the evolving Cambrian fitness landscape. The primary question in this integrated causal hypothesis now remains the timing and absolute magnitude of hypothesized late Neoproterozoic oxygenation. Continued exploration of the causes, timing, and magnitude of oxygenation will provide further insight into the role of oceanographic change in the evolution of carnivory and this unique geobiological event. Further study of the relationship between feeding ecology and oxygen in modern OMZs, as well as the coevolutionary history of animals and ocean redox state in deep time, may also help us predict future changes associated with ocean deoxygenation and expanding oxygen minimum zones (46).

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