TACKLING THE 99%: CAN WE BEGIN TO UNDERSTAND THE PALEOECOLOGY OF THE SMALL AND SOFT-BODIED ANIMAL MAJORITY?

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ABSTRACT.—Not all organisms have an equal chance of entering the fossil record. Previo—us attempts to quantify this percentage suggest that for megascopic marine organisms (megafauna), ~30% would be predicted to leave no identifiable fossils. Here, that exercise is repeated for marine macrofauna, for which ~80% are predicted to leave no identifiable fossils. The percentage will be far higher for meiofauna, the numerically most dominant marine animals. The organisms which are often most abundant in marine sediments, such as small polychaetes and nematodes, have essentially no fossil record. Yet such organisms are ecologically important in the modern oceans, and almost certainly were in ancient environments as well, so it is useful to consider the roles they play in different ecosystems. Insight into the evolution and paleoecology of these groups can be gained by using molecular divergence estimates to infer temporal origins combined with modern distributional and ecological data. As a case study, this approach is applied to the small and soft-bodied early animal fauna living under low levels of atmospheric oxygen that likely characterized the Precambrian.

INTRODUCTION

"Here we have a fossil: what went wrong?"

—Adolf Seilacher (2006, Extraordinary Glimpses of Past Life course, Yale University)

Fossils preserve an imperfect record of the history of life because organisms lacking easily fossilizable hard parts have a difficult chance of entering the fossil record. But Seilacher's insight, said while holding a common mollusk fossil, reminds us that it is not just soft-bodied organisms that are unlikely to leave fossils. Even shelly remains may break, abrade, and dissolve before ever becoming a permanent part of strata, and, if fossilized, must then survive erosion and/or metamorphism before the fossil remains are found. The stratigraphic record at any one place is, after all, "...one long gap with only occasional sedimentation" (Ager, 1973, p. 34). Fossils are, in this view, an error of nature, and questions of taphonomy and bias must be at the forefront when making any observation about paleoecological patterns.

Given this fact, it would be interesting to know what percentage of a given fauna will likely enter the fossil record under the best of circumstances. In a seminal study of the megascopic intertidal fauna at Friday Harbor, Washington, Schopf (1978) predicted that ~30% of species would leave many identifiable fossils, regardless of whether they lived on mud, sand, or rock. He further predicted that ~40% of the fauna would leave few identifiable fossils, and the remaining ~30% would leave no identifiable fossils. In a similar exercise using an ancient, exceptionally preserved fauna, Briggs (1991) used a faunal reconstruction by Conway Morris and Whittington (1985) to estimate that ~14% of species in the Middle Cambrian Burgess Shale would have been preserved under normal taphonomic circumstances.

These calculations are presumably correct with regard to the question addressed (specifically large, easily visible animals), but ignore what turns out to be the statistical mode of animal life in the oceans: small worms with a length scale of millimeters and a width scale of several tens of microns. Schopf (1978, p. 262) explicitly limited his study to "the modern counterpart of the animals which paleontologists might expect to find in an outcrop," omitting "...turbellarians, nematodes, nearly all small crustacea, tiny annelids, protozoa, etc." Regarding the Burgess Shale example, it is true that exceptionally

preserved biotas offer windows into the biology and paleoecology of soft-bodied organisms (Bottjer et al., 2001), but for as-yet unclear reasons, the very small organisms that comprise the majority of animals do not fossilize readily. Burgess Shale preservation is spectacular, but no millimeter-scale worms are preserved (Briggs et al., 1994), even though they may have been living in the Burgess mud. The canonical studies of Schopf (1978) and Briggs (1991) have strongly influenced perceptions in the field of what proportion of the marine fauna is preserved, or can be preserved, under normal circumstances. Nature has so rarely 'failed' (to use Seilacher's terminology) to obliterate tiny organisms such as nematodes from the fossil record that they scarcely enter paleontologists' collective conscience.

For comparison with the analyses of Schopf (1978), the percentage of the entire modern marine fauna that is likely to enter the fossil record has been calculated. This exercise is meant to be illustrative rather than exhaustive, although the faunal data span a range of depth, oxygen, and temperature conditions representative of the geological past. Faunal lists were obtained from four ocean-margin transects (Gallardo et al., 2004; Palma et al., 2005; Levin et al., 2010; Ingole et al., 2010) where the identity and abundance of macrofauna (defined in these studies as organisms retained on a 300 μm sieve) was quantified. In marine benthic ecology studies, macrofauna are the intermediate size class between megafauna, which can be seen in sea floor photographs, and meiofauna, which pass through a 300 μm sieve but are retained on a 40 μm sieve (although it is important to note that the exact sieve sizes employed may vary between research groups/ regions). Faunal lists were coded using the categories of Schopf (1978), with the exception that jawed polychaetes were predicted to yield no identifiable fossils instead of some identifiable fossils. Although polychaete jaws can be found in the fossil record (e.g., Hints and Eriksson, 2007), they are rarely reported, either because they are rare or are underutilized in discussions of paleoecology relative to other fossils in this category, such as sponge spicules.

The data from these four surveys (34 stations total) show a very different pattern for macrofauna compared to megafauna (Fig. 1A versus Fig. 1B, C). Whereas ~30% of the megafauna were considered unlikely to yield any identifiable fossils (Schopf, 1978), the
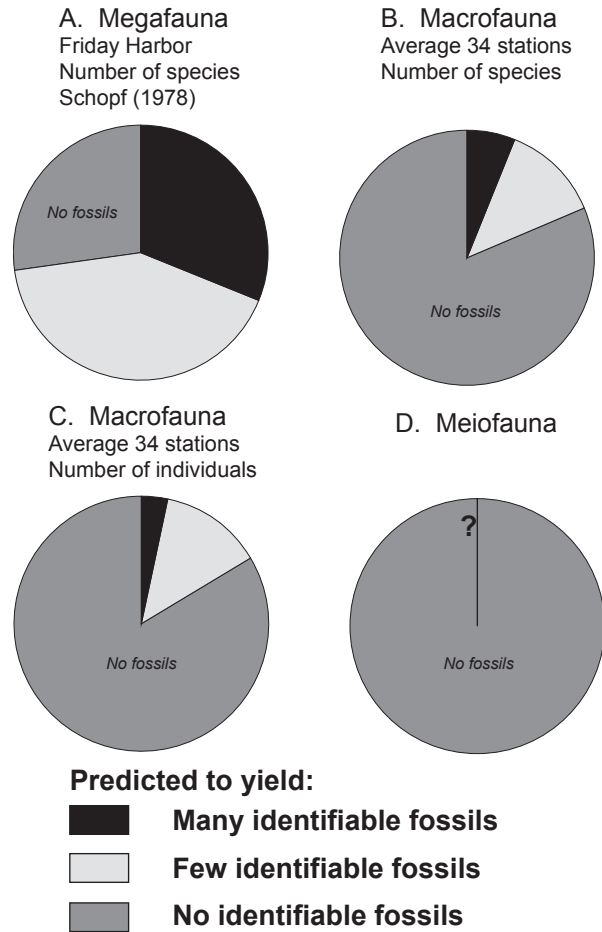

Predicted to yield:

■ **Many identifiable fossils**

□ **Few identifiable fossils**

▨ **No identifiable fossils**

FIGURE *1*.—Proportion of taxa predicted to leave many fossils, few fossils, or no fossils. A) Megafauna or megascopic animals (Schopf, 1978), i.e., those visible in visual or photographic ecological surveys. B) Macrofauna (animals retained on a > 300 μm sieve); average from 34 modern ocean stations, analyzed by number of species. C) Macrofauna; average from 34 modern ocean stations, analyzed by number of individuals. D) Meiofauna (< 300 μm but > 40 μm); the percentage of meiofauna likely to leave fossils is unknown, but certainly very small; with rare exceptions, meiofauna do not enter the fossil record.

comparable figure for macrofauna was ~80%. This contrast holds true both for number of species and number of individuals (Fig. 1B, C). The percentage of animals likely to enter the fossil record is even less if the meiofauna are considered. Some meiofauna, such as ostracodes, are preserved in the fossil record, and their study has led to important insights about evolutionary process (Hunt and Roy, 2006). However, the vast majority of meiofauna consists of nematodes (Brusca and Brusca, 2003), which apparently do not fossilize in the marine realm and are

preserved in the terrestrial realm only under the rarest of circumstances (discussed below; Poinar et al., 1994; 2008). Because quantitative meiofaunal studies are relatively rare, and because meiofauna are all essentially unfossilizable, a quantitative comparison with Schopf (1978) was not repeated for these organisms. However, because there are thousands of meiofaunal animals in every square meter of marine sediment (e.g. Neira et al., 2001b), it is apparent that less than 1% of marine animals have the potential to enter the fossil record.

Despite an imperfect record of macrofauna and meiofauna, as a field, paleobiology has gained a strong first-order understanding of the history of life on Earth. Yet while the small-bodied majority may be paleontologically invisible, they are not paleoecologically unimportant, and it is useful to try to understand the roles they play in the ecosystem. These organisms have important roles in organic matter processing and pellet formation, affecting sediment properties (e.g., Neira and Hoppner, 1994; Wild et al., 2005). Certain macrofauna also play a key role in rapidly transporting organic matter deeper into the sediment, supporting subsurface deposit- and detritus-feeding communities (Levin et al., 1997). The burrowing activities of these organisms are also important in affecting community composition, as deposit-feeding macrofauna may rework the sediment so extensively that they prevent suspension-feeding organisms or epifauna from coexisting in the same habitat (reviewed by Meadows et al., 2012). Also, not all burrows are created equal; experiments by Shaikh et al. (1998) demonstrated that a mud-burrowing crustacean caused transitional failure of the seafloor, whereas a mud-burrowing polychaete produced block-and-wedge failure, thus creating different niches on the failed slope. The role(s) of meiofaunal burrowing on the seafloor are essentially unknown—Meadows et al. (2012, p. 39) stated, "the current authors know of no published work that specifically addresses this neglected group of marine benthic organisms in terms of the role as ecosystem engineers," but cite Murray et al. (2002, p. 22) as noting that marine benthic nematodes "...may be the single most important biogeomorphological agent on the planet…" From a geochemical perspective, burrows increase solute transport into the sediment, even on the meiofaunal level (Aller and Aller, 1992; Green and Chandler, 1994), and the abundance of small burrows plays an important

role in sedimentary geochemistry and re-oxidation of reduced geochemical species (Aller, 1980; 1994; Aller and Yingst, 1985). Perhaps most importantly from a paleoecological standpoint, they form an important trophic link between sedimentary organic matter/detritus and higher carnivores. The question is how to gain paleoecological insights for groups with no fossil record. Here, it is suggested that modern molecular methods for estimating divergences, combined with modern distributional and environmental data, can begin to provide information about paleoecological questions of the 99% in deep time.

ESTIMATING THE TEMPORAL ORIGINS OF SOFT-BODIED ANIMAL GROUPS

The central idea behind the molecular clock model was first proposed in the 1960s by Zuckerkandl and Pauling (1965). They recognized that if the time of divergence of specific nodes on the metazoan tree could be calibrated from the fossil record, rates of molecular evolution with respect to time could be determined, and these rates then applied to other nodes. This approach was first applied to the deep metazoan fossil record by Runnegar (1982), who estimated that the last common ancestor of bilaterians diverged ~900–1000 million years ago. The early history of molecular clock studies resulted in a range of findings. Subsequent to Runnegar's (1982) attempt, estimates of the age of bilaterian divergence using different techniques spanned over one billion years of earth history. Problems included: 1) poor estimation of branch lengths due to unsophisticated models of evolution; 2) misleadingly small estimation of confidence intervals; 3) calibration points that were geologically inaccurate or derived from previous molecular clock studies; and 4) analyses based on few genes and few taxa—often only 18S ribosomal DNA (reviewed by Bromham, 2003; Graur and Martin, 2004). Summing up molecular clock estimates for the last common ancestor of bilaterians in the early 2000s, Gould (2002, p. 1155) wrote, "...the current literature seems too labile for a conclusion."

The result was that molecular clock estimates were often disregarded by paleontologists. Modern methods, however, are much improved, such that most estimates are very similar to those derived from the fossil record (see below). The most important advance is that modern molecular
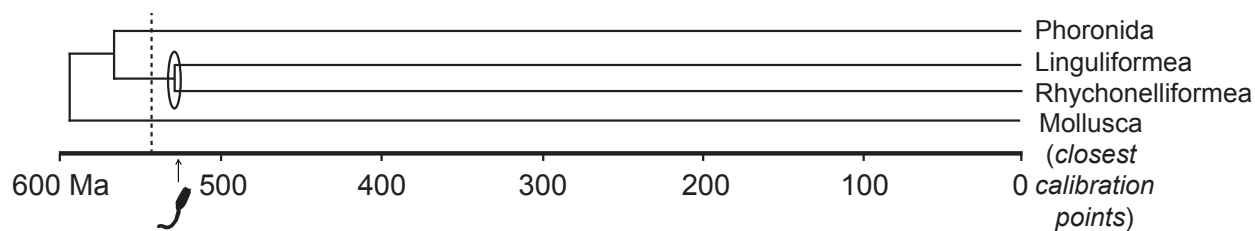
FIGURE *2*.—Concordance of modern molecular divergence estimates with the fossil record in the absence of internal calibration points. Erwin et al. (2011) used no brachiopod calibration points, and of 24 total calibration points, the closest external calibration points were in the Mollusca. The estimated age for the divergence of the Linguliformea and Rhychonelliformea (crown-group Brachiopoda; circled node) closely matches the most recent estimate for this node from the fossil record (arrow). Dashed vertical line is Precambrian–Cambrian boundary at 542 Ma.

divergence estimation methods now explicitly take into account the fact that rates of molecular evolution vary between lineages (Drummond and Rambaut, 2007; Lepage et al., 2007; Lartillot et al., 2009). In other words, these analyses are not strictly a molecular clock, and no single rate of molecular evolution is assumed. Modern studies have also taken advantage of complex site-heterogeneous models to infer branch lengths (e.g., the CAT-based models in the program Phylobayes; Lartillot and Phillppe, 2004; Lartillot et al., 2009), and date phylograms derived from many genes and many more taxa than previously available (albeit still representing a very small percentage of the total living fauna). Finally, fruitful collaborations between paleontologists and molecular evolutionists regarding how to correctly define and model the geological uncertainty around calibration points has begun to emerge (Parham et al., 2012).

These improvements have resulted in molecular divergence estimates that are both generally reproducible between studies, and much more consistent with the fossil record. As an example, Erwin et al. (2011) estimated molecular divergences for 118 metazoan taxa using seven nuclear housekeeping genes and 24 calibration points. The study included genetic data from multiple brachiopod species, but no calibration points from within the Brachiopoda, so that they could serve as a test case for the geological accuracy of the molecular clock. In essence, the brachiopod results were the same as if the group were a soft-bodied taxon with no fossil record. The brachiopod crown group (circled node on Figure 2) is defined by the last common ancestor of Linguliformea and Rhychonelliformea (Carlson, 1995; Holmer et al., 1995). This node was dated to 530 Ma (average of analyses in Fig. 1 and figs. S2–4 of Erwin et al., 2011; see also

results of Sperling et al., 2011). The most recent estimate for this divergence (arrow in Figure 2) based on the fossil record is 527 Ma (Maloof et al., 2010). These ages are very close, and the genetic divergence slightly predates the first appearance of the fossils, as would be expected given that the very first fossil is unlikely to be preserved and/or found—the so-called 'Spill-Rongis' effect (Marshall, 1995). This test case is important for soft-bodied organisms in demonstrating that even when only calibration points external to a clade are used, a geologically accurate result can still be obtained.

The apparent geological accuracy of this example does not imply that all molecular divergence estimates are necessarily accurate. However, the field has clearly matured to the point where hypotheses of clade origins from both the fossil and molecular records are congruent, and the remaining discordances can yield new insights into the fossil record, the molecular record, or both (Peterson and Butterfield, 2005; Peterson et al., 2007; Sperling et al., 2010; Anderson et al., 2011). Most important for understanding the evolution of soft-bodied groups, molecular methods can, with some accuracy, date the origin of clades even if they have no fossil record, as shown by the brachiopod example that used only external calibration points. Dating origins of soft-bodied clades, especially paraphyletic groups (see fig. 1 of Sperling et al., 2007), can give insight into the temporal origins of different body plans in these groups. Although molecular divergence estimates for soft-bodied groups must be regarded with skepticism because there is no independent test from the fossil record, within the context of the associated analytical uncertainty, they do offer a window into the temporal origins of these clades that would otherwise be unavailable.

ECOLOGY OF THE SOFT-BODIED MAJORITY

Molecular divergence estimates only give insight into the time of origin of a clade and not abundance or ecological function. Although inferential, it is possible to use distributional and ecological data from extant representatives and environmental analogs to make hypotheses about the composition of soft-bodied communities in the fossil record, as well as their roles in the ecosystem. Macrofauna, and to a lesser extent, meiofauna, have been studied by marine biologists and ecologists in essentially all possible modern habitats, leading to a large body of knowledge to draw upon. Here, an example is given using the macrofaunal organisms living in modern Oxygen Minimum Zones (OMZs) to infer the potential characteristics of early animal communities under the low atmospheric oxygen levels that characterized the Precambrian. Although absolute oxygen levels are not known with certainty, most workers generally agree that Precambrian oxygen levels were ~1–10% of modern levels (see Canfield, 2005; Kump, 2008), and that seafloor anoxia was much more pervasive than in the modern oceans (Reinhard et al., 2013).

Case study: the paleoecology of early animal communities

The exact timing of the origin of animals is still a matter of controversy. Recent molecular divergence analyses suggest crown-group animals diverged ~780 Ma, and bilaterian animals diverged ~670 Ma (Erwin et al., 2011). While the confidence intervals on these estimates are fairly wide, the youngest 95% confidence interval for both nodes still remains entirely within the Cryogenian, and a pre-Ediacaran origin of animals is supported by presumed demosponge-specific biomarkers in the South Oman Salt Basin (Love et al., 2009). Further evidence for these ages comes from the Ediacaran fossil *Kimberella*, which is assumed to be an early representative of the Mollusca or the Lophotrochozoa (Fedonkin and Waggoner, 1997). Given the derived positions of these clades in the metazoan tree and the age of *Kimberella* (at least 555 Ma; Martin et al., 2000), any reasonable estimate of molecular evolution would imply that the Bilateria and Metazoa have a much deeper history.

The early divergence of animal lineages raises a conundrum: there are few convincing animal fossils and no convincing bilaterian fossils or trace fossils from the early Ediacaran or Cryogenian (Erwin et al., 2011, and references therein). A common hypothesis to explain this pattern is that under low levels of atmospheric oxygen that likely characterized the Precambrian (Kump, 2008), early animals were entirely soft-bodied, low in abundance, and did not fossilize (Cloud, 1968; Rhoads and Morse, 1971; Fortey et al., 1996; Knoll and Carroll, 1999; but see discussion by Budd and Jensen, 2000). There is a clear theoretical relationship between body size and oxygen levels (Raff and Raff, 1970; Alexander, 1971; Runnegar, 1991; Payne et al., 2010), and, as hinted at above with respect to nematodes, the lack of fossils in the Precambrian paleontological record—at least with respect to the body fossil record—would not be surprising if animals were entirely small and soft-bodied. Despite dominating modern sediments by abundance (Brusca and Brusca, 2003), nematodes simply are not preserved in the marine fossil record. The only reported fossil marine nematode, *Nemavermes mackeii* from the Mazon Creek fauna (Schram, 1973), is probably not a nematode, as it is orders of magnitude larger than modern marine nematodes and, more importantly, does not share any synapomorphic characters with modern nematodes. Nematodes are only preserved in truly exceptional circumstances, such as in amber or by silica permineralization in hot springs (Poinar et al., 1994, 2008). The earliest bilaterians may have been slightly larger than nematodes (at least 3 millimeters long as opposed to 1 millimeter long; see discussion in Budd and Jensen, 2000), but the fact that capitellid polychaetes, which are abundant in modern settings, are never preserved as fossils indicates the same logic can be applied to more complex models for the last common ancestor of bilaterians.

To investigate whether such a model for the absence of true metazoan or bilaterian fossils (Cloud, 1968; Rhoads and Morse, 1971; Fortey et al., 1996; Knoll and Carroll, 1999) makes sense, the biota of modern Oxygen Minimum Zones (OMZs) can be used as an analogue for Precambrian animal communities. In modern oceans, OMZs form under areas of high primary productivity, such as upwelling zones, leading to intense organic carbon remineralization in the water column, and consequently, very low oxygen levels. Because OMZs are geologically long-lasting oceanographic features, organisms living

in them have had time to adapt, and thus they serve as good—although not perfect—analogues for times in Earth history with lower levels of atmospheric oxygen or more widespread reducing conditions (Rhoads and Morse, 1971; Sperling et al., 2013b).

Investigation of modern OMZs demonstrates that animals are not excluded from the sediment until extremely low oxygen levels are reached (< 0.02 ml/l O_2 or < 0.3% modern surface ocean concentrations; Sperling et al., 2013b). Although low oxygen levels do not completely prohibit the presence of animals, oxygen does play an important role in organism size, diversity, and trophic ecology. In concordance with theoretical modeling, there is a decrease in animal size in cores of OMZs (Rhoads and Morse, 1971; Levin, 2003; Gooday et al., 2009). The fauna at the lowest oxygen levels are characterized almost entirely by very small and thin nematodes and polychaetes. Such body plans are required to maximize surface-area-to-volume ratios for increased diffusion, and respiratory structures commonly are further enlarged for higher O_2 uptake (Lamont and Gage, 2000; Neira et al., 2001a, Jeffreys et al., 2012). A second feature of faunas found at very low O_2 levels is that most of the organisms are not biomineralized (Levin, 2003). The reasons for this are currently unclear: possibilities include a metabolic cost to biomineralization; high CO_2 levels in modern OMZs, where low O_2 is a result of intense organic carbon remineralization; and a lack of predation pressure. In essence, the fauna characterizing modern OMZ cores is the soft-bodied, and generally unfossilizable, majority. Under low oxygen levels, and considering the fossil record of groups like nematodes and capitellid polychaetes, a pre-Ediacaran origin of bilaterians as inferred from molecular divergence estimates is not actually discordant with the Precambrian body fossil record.

Low oxygen levels not only affect body size in OMZs, but also shape the ecological structure of OMZ communities in a fairly complex manner. At the very lowest O_2 levels (i.e., < 0.1 ml/l O_2, or ~ 2% of surface ocean concentrations), both organismal abundance and species-level diversity is depressed (Levin and Gage, 1998; Levin, 2003; Gooday et al., 2010). These communities have high dominance, generally with only one to a few species present. At slightly higher O_2 levels (~0.1–0.5 ml/l O_2), 'edge effects' (Mullins et al., 1985) can be seen in which a combination of high food availability, release from oxygen limitation, and low predation pressure results in extraordinarily high organismal densities (often ~20,000+ individuals/m^2; Levin, 2003), but with diversity still dominated by a few opportunistic species. Diversity then increases with increasing oxygen, and at oxygen levels > 1 ml/l, oxygen is less important in shaping communities than other environmental and ecological factors (e.g., Levin and Gage, 1998).

A third correlate of low-oxygen levels in modern OMZs is the absence of predation and short food chains. This phenomenon was recently quantified by Sperling et al. (2013a), who investigated how polychaete feeding strategies in OMZs varied with oxygen levels. Polychaetes were chosen as the study taxon because 1) they are the most abundant macrofaunal-sized animals in OMZs (Levin, 2003); 2) they have a diversity of feeding modes including surface and subsurface deposit feeders, detritivores, filter feeders, and carnivores; 3) their feeding biology is relatively well known; and 4) polychaetes are among the most low-oxygen tolerant organisms in the modern biota (Levin, 2003), making them a conservative choice with respect to oxygen influence. The study found that lower oxygen levels were correlated with both low percentages of carnivorous individuals in a fauna and low numbers of carnivorous species, indicating less complex food webs. For the lowest oxygen stations (< 0.2 ml/l O_2), almost half the stations lacked carnivorous polychaetes, whereas all stations above 0.34 ml/l O_2 had carnivorous polychaetes present (Sperling et al., 2013a). Of the organisms in these very low-oxygen faunas, most are detritivores or deposit feeders (Sperling et al., 2013a)—the lack of filter-feeders is probably related to the muddy, soupy substrates that often characterize OMZs rather than any physiological cause (Levin, 2003).

Consequently, using a uniformitarian approach, a number of inferences can be made about how early animal communities living under 1–10% present atmospheric levels (PAL; cf. Kump, 2008) may have been structured. Precambrian animals were likely small, thin, organisms with enhanced respiratory surface area for increased oxygen diffusion. Communities likely would have had relatively low abundances with respect to normal, modern, open-marine fauna, low diversity, and high dominance. Finally, these communities likely would have had very short, if not single-tiered, trophic chains, with

animals directly ingesting organic detritus or deposit-feeding.

CONCLUSIONS

Any attempt to truly understand the paleoecology of the small and soft-bodied animal majority will be, at the least, inferential. For marine clades that do not fossilize, such as nematodes, we are left with molecular divergence estimates for times of clade origins and a uniformitarian exercise in extending modern ecological patterns to the geological past. Nonetheless, it is argued here that modern molecular divergence estimates are robust, and, at least at a broad scale, modern ecology does have applicability to deep time. Particularly, recent benthic ecology studies of OMZs can give insight into the paleoecology of ancient low-oxygen settings, from threshold-effect changes in organic matter processing in organic-rich sediments (e.g., Woulds et al., 2007), to the broad characteristics of Precambrian animal life (Sperling et al., 2013a, b). Although animals likely originated as small and soft-bodied in the Precambrian, this body form and numerical dominance did not disappear with the arrival of macroscopic shelly organisms, and small and soft-bodied continues to be the majority bauplan of animal life. Future advances in molecular divergence estimates and the ecology of extant macro- and meiofauna, combined with taphonomic experiments on small, soft-bodied animals and targeted searches for promising environments in the geological record, will give increased insight into the evolutionary and ecological history of these organisms.

However, while this approach gives a roadmap for understanding the paleoecology of soft-bodied animals, ultimately this paper is less of a manifesto for a research program in the paleoecology of the 99%, and more of a reminder to remember the soft-bodied majority while considering questions of the 1% that can be robustly addressed with the fossil record. Specifically, every hand sample of sedimentary rock was once sediment with a fauna consisting not only of the fauna that is preserved, but tens, hundreds, or thousands of soft-bodied organisms that never entered the fossil record, yet were important in sediment and organic-matter processing, and as a trophic link to higher levels. The structure and effect of this soft-bodied community varies widely in the modern oceans, and remaining cognizant of possible differences in ancient soft-bodied communities between different environments may be useful in better understanding overall paleoecological patterns.

ACKNOWLEDGMENTS

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