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Tempo and mode of early animal evolution: inferences from rocks, Hox, and molecular clocks

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Abstract.—One of the enduring puzzles to Stephen Jay Gould about life on Earth was the cause or causes of the fantastic diversity of animals that exploded in the fossil record starting around 530 Ma—the Cambrian explosion. In this contribution, we first review recent phylogenetic and molecular clock studies that estimate dates for high-level metazoan diversifications, in particular the origin of the major lineages of the bilaterally-symmetrical animals (Bilateria) including cnidarians. We next review possible ''internal'' triggers for the Cambrian explosion, and argue that pattern formation, those processes that delay the specification of cells and thereby allow for growth, was one major innovation that allowed for the evolution of distinct macroscopic body plans by the end of the Precambrian. Of potential ''external'' triggers there is no lack of candidates, including snowball earth episodes and a general increase in the oxygenation state of the world's oceans; the former could affect animal evolution by a mass extinction followed by ecological recovery, whereas the latter could affect the evolution of benthic animals through the transfer of reduced carbon from the pelagos to the benthos via fecal pellets. We argue that the most likely cause of the Cambrian explosion was the evolution of macrophagy, which resulted in the evolution of larger body sizes and eventually skeletons in response to increased benthic predation pressures. Benthic predation pressures also resulted in the evolution of mesozooplankton, which irrevocably linked the pelagos with the benthos, effectively establishing the Phanerozoic ocean. Hence, we suggest that the Cambrian explosion was the inevitable outcome of the evolution of macrophagy near the end of the Marinoan glacial interval.

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> The Cambrian explosion ranks as such a definitive episode in the history of animals that we cannot possibly grasp the basic tale of our own kingdom until we achieve better resolution for both the antecedents and the unfolding of this cardinal geological moment.
>
> [Gould 1998]

Introduction

The Cambrian explosion stands out, both in the history of animal evolution and in the writings of Stephen Jay Gould, as the pivotal event in animal evolution. Although multifarious like no other episode in the history of life, Gould saw three particularly important evolutionary issues associated with the Cambrian explosion: (1) the rapidity of morphological evolution in the Early Cambrian, and its independence from genealogy; (2) the cause of this rapidity, whether triggered environmentally or genetically; and (3) the notion of disparity, or the stability of animal body plans over the ensuing 530 million years. Although this stability is, according to some (e.g., Levinton 2001), the single most important fact the fossil record has contributed to the science of evolutionary biology, here we will restrict our discussion to the first two themes, whether the anatomical innovations characterizing numerous groups were separate from the events generating the clades, and the nature of the triggers causing the innovations because these two issues are obviously entwined. As Gould (2002) argued: if only a single Early Cambrian lineage generated all Cambrian diversity, then an internal trigger based upon some genetic or developmental ''invention'' is plausible; if, alternatively, most phylum-level lineages were already established well before the Precambrian/Cambrian boundary, then their transformation into the larger and well-differ-

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entiated body plans, apparent by the Atdabanian, suggests some sort of external trigger. Our goals here are to (1) place the evolutionary history of animals into a proper phylogenetic and temporal context; (2) address the notion of internal versus external triggers to the Cambrian explosion; and (3) summarize early animal evolution in the context of the late Precambrian to Cambrian transition.

Clocks: How Many Worms Crawled across the Precambrian/Cambrian Boundary?

> The Cambrian explosion, as paleontologists propose and understand the concept, marks an anatomical transition in the overt phenotypes of bilaterian organisms—that is, a geologically abrupt origin of the major *Baupläne* of bilaterian phyla and classes—not a claim about times of initial phyletic branching. (Gould 2002)

Of considerable interest to Gould was the conflict between two competing views of the Cambrian explosion: whether the Cambrian explosion reflects the rapid appearance of fossils with animals having a deep, but cryptic, Precambrian history, as suggested by most molecular clock studies; or whether it reflects the true sudden appearance and diversification of animals, as suggested by a literal reading of the fossil record (see Runnegar 1982). Although Gould stressed that the Cambrian explosion stands as one of the most important evolutionary events in natural history irrespective of when the lineages actually diverged from one another, a deeper understanding of the mechanisms underlying the Cambrian explosion requires knowledge about how these lineages are interrelated, and when in time the lineages themselves came into existence.

Metazoan Phylogeny.—With the advent of molecular systematics, much progress has been made in our understanding of how animals are related to one another. Figure 1 shows a maximum parsimony analysis of 28 metazoan species, plus five non-metazoan taxa, based on a concatenation of 2039 amino acid positions derived from seven different housekeeping genes, 228 amino acid positions from the cytochrome oxidase I gene, 1747 nucleotide characters from the 18S rDNA gene, and 155 morphological characters coded for the genus where possible (Peterson unpublished). This ''total evidence'' tree supports the monophyly of both well-and newly-established nodes including all recognized phyla, Metazoa, Deuterostomia (represented here by echinoderms and hemichordates), Trochozoa (nemerteans, annelids, and molluscs), Platyzoa (the rotifer and the flatworm), Spiralia (the trochozoans and the platyzoans), Ecdysozoa (the priapulid and the insects), and Protostomia (the spiralians and the ecdysozoans) (e.g., Halanych et al. 1995; Aguinaldo et al. 1997; Zrzavy et al. 1998; Giribet et al. 2000; Peterson and Eernisse 2001; Mallatt and Winchell 2002; reviewed in Eernisse and Peterson 2004).

As expected, we find strong support for the monophyly of triploblasts, those bilaterians possessing true mesoderm. Recent studies on cnidarians have demonstrated that mesoderm is a triploblast apomorphy because ''mesoderm'' genes are expressed in the endoderm of the anthozoan *Nematostella* (Scholtz and Technau 2003; Martindale et al. 2004) and are not absent as would be expected if mesoderm was secondarily lost. We also find strong support for the clade Cnidaria + Triploblastica, a clade we will refer to, somewhat unconventionally, as ''Bilateria,'' because it appears that bilateral symmetry is primitive for Cnidaria and Triploblastica and is still present in anthozoans, as assessed by both morphological and genetic criteria (Hayward et al. 2002; Finnerty et al. 2004). Finally, we find weak support for the monophyly of Eumetazoa (Ctenophora + Bilateria), which suggests that tissues, the nervous system, and importantly a true gut each evolved once, contra the hypothesis of Cavalier-Smith et al. (1996).

Two phylogenetic results are particularly important for what is to follow. First, we do not find a monophyletic Porifera, consistent with most recent ribosomal analyses (Borchiellini et al. 2001; Medina et al. 2001; Peterson and Eernisse 2001; but see Manuel et al. 2003). In particular, those sponges whose skeletons are composed of calcareous spicules (Calcispongia) are the sister taxon of Eumetazoa, whereas the remaining sponges, whose

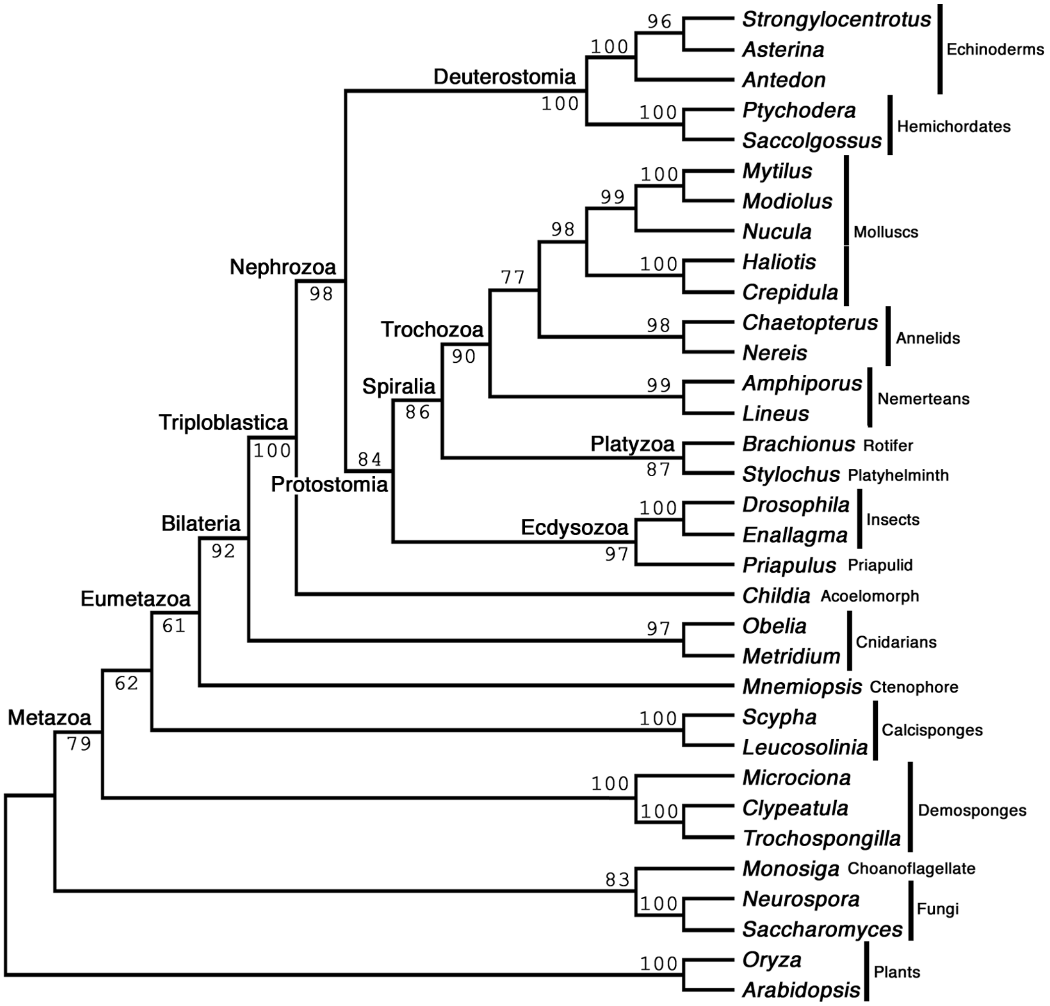

FIGURE 1. Maximum parsimony analysis (PAUP v. 4.0b10 for Macintosh [Swofford 2002]) of a total-evidence data set consisting 2039 amino acid positions derived from seven different housekeeping genes (Peterson et al. 2004), 228 amino acid positions from the cytochrome oxidase I gene, 1747 nucleotide characters from the 18S rDNA gene, and 155 morphological characters coded for the genus where possible, for 28 metazoans, the choanoflagellate *Monosiga*, two fungi, and two plant taxa. The tree is 13,266 steps long (number of parsimony informative characters = 1989); C.I. = 0.50; R.I. = 0.48; R.C. = 0.24. Bootstrap percentages are derived from 1000 replicates. Of particular importance is the paraphyly of Porifera with calcisponges more closely related to eumetazoans than to demosponges, and the basal position of the acoel flatworm *Childia* with respect to the other triploblasts. (From Peterson unpublished.)

skeletons are composed of siliceous spicules (Silicispongia = Demospongia + Hexactinellida), are the sister taxon of the Calcispongia + Eumetazoa clade. This result is not driven solely by the ribosomal sequences, as the paraphyly of Porifera is also found when the amino acid sequences of the seven different housekeeping genes are analyzed by Minimum Evolution alone (Peterson and Butterfield unpublished). An obvious implication of these results is that both the last common ancestor of Metazoa, and the last common ancestor of Calcispongia + Eumetazoa were constructed like a modern sponge, an obligate benthic organism with a water-canal system (Eernisse and Peterson 2004).

Second, the acoel flatworm *Childia* falls at the base of the triploblasts with high precision, again consistent with virtually all recent phylogenetic inquiries (Ruiz-Trillo et al. 1999, 2002; Jondelius et al. 2002; Pasquinelli et al. 2003; Telford et al. 2003). Acoels are direct-developing, micrometazoan acoelomates, suggesting that the earliest triploblasts were also small, benthic, directly developing animals with internal fertilization and a uniphasic life cycle (i.e., eggs laid on the benthos, not released into the pelagos) (Baguñà et al. 2001; Jondelius et al. 2002). An important implication is that both coeloms (contra Budd and Jensen 2000) and complex life cycles (contra Peterson et al. 2000, see below) arose multiple times within the clade Nephrozoa (all triploblasts exclusive of acoelomorphs, and which primitively possess nephridia [Jondelius et al. 2002]).

Our analysis does not consider the phylogenetic position of nematodes. This is a contentious issue because nematodes are placed within the Ecdysozoa on the basis of ribosomal sequence analysis (Aguinaldo et al. 1997; Peterson and Eernisse 2001; Mallatt and Winchell 2002; Mallatt et al. 2004), the possession of ecdysozoan-specific posterior Hox genes (de Rosa et al. 1999), and a nervous system with HRP immunoreactivity (Haase et al. 2001), whereas genome-wide phylogenetic analyses support a basal triploblast position (Blair et al. 2002; Wolf et al. 2004). Nonetheless, given the amount of gene loss in the *C. elegans* system, it is difficult to say where exactly nematodes fall within Triploblastica, although an affinity with the fruit fly *Drosophila* is not ruled out (Copley et al. 2004). Despite this controversy, it makes little difference to our arguments; in fact, a basal triploblast position would only reinforce the conclusions reached herein.

The Geologic Time Frame.—In order to relate animal evolution to terminal Neoproterozoic geology and the metazoan fossil record, accurate and precise geochronological dates are required. Probably the most important date of all is the formally defined Proterozoic/Cambrian boundary (Landing 1994), which was calibrated to 543–542 Ma by precise U-Pb zircon geochronology on correlative sections in Siberia (Bowring et al. 1993), Namibia (Grotzinger et al. 1995), and Oman (Amthor et al. 2003). The spectacular embryos entombed in chert and phosphate of the Doushantuo Formation in southern China (Xiao et al. 1998; Li et al. 1998), which represent the oldest known unequivocal metazoan remains, are suggested to be less than 580 Myr old. The first appearance of macroscopic Ediacara fossils—including giant frondose specimens up to 2 m long—is within the 575 Ma Drook Formation in southeast Newfoundland (Narbonne and Gehling 2003). These ancient Ediacara lineages continue upsection to the Mistaken Point deposits dated at 565 Ma (Benus 1988). Finally, macroscopic bilaterians make their first appearance at 555 Ma (Martin et al. 2000). These ages are shown on Figure 2 and are listed in Table 1.

A New Metazoan Time Frame.—Using the topology in Figure 1 as our phylogenetic framework, and the high-precision geochronological dates reviewed above, we can now discuss the time frame for bilaterian evolution. The molecular clock is the tool of choice to test hypotheses of metazoan originations independent of the fossil record (Runnegar 1982). Although problems exist with certain aspects of molecular clock analyses (Smith and Peterson 2002; Benton and Ayala 2003), two recent analyses came to the same conclusion: bilaterians arose ca. 600–630 Ma, and nephrozoans arose ca. 560–580 Ma (Aris-Brosou and Yang 2002, 2003; Peterson et al. 2004; see each individual paper for details of the analyses and confidence intervals). The estimates from an updated analysis of Peterson et al. (2004; Peterson unpublished) are shown on Figure 2.

These dates differ from almost every previous molecular clock study, many of which argue that the last common ancestor of Nephrozoa originated ca. 1000 Ma (e.g., Wray et al. 1996; Bromham et al. 1998; Wang et al. 1999; Nei et al. 2001), because the rate of molecular evolution across taxa was addressed in detail. Peterson et al. (2004) examined seven new protein sequences from over 20 new taxa, which allowed for the use of multiple calibration points scattered across bilaterian phylogeny and through time, whereas Aris-Brosou and Yang (2002, 2003) undertook sophisticated analyses of published sequences using a Bayesian posterior-probability approach to account for rate heterogeneity. Importantly, both groups of authors demonstrated the ex-

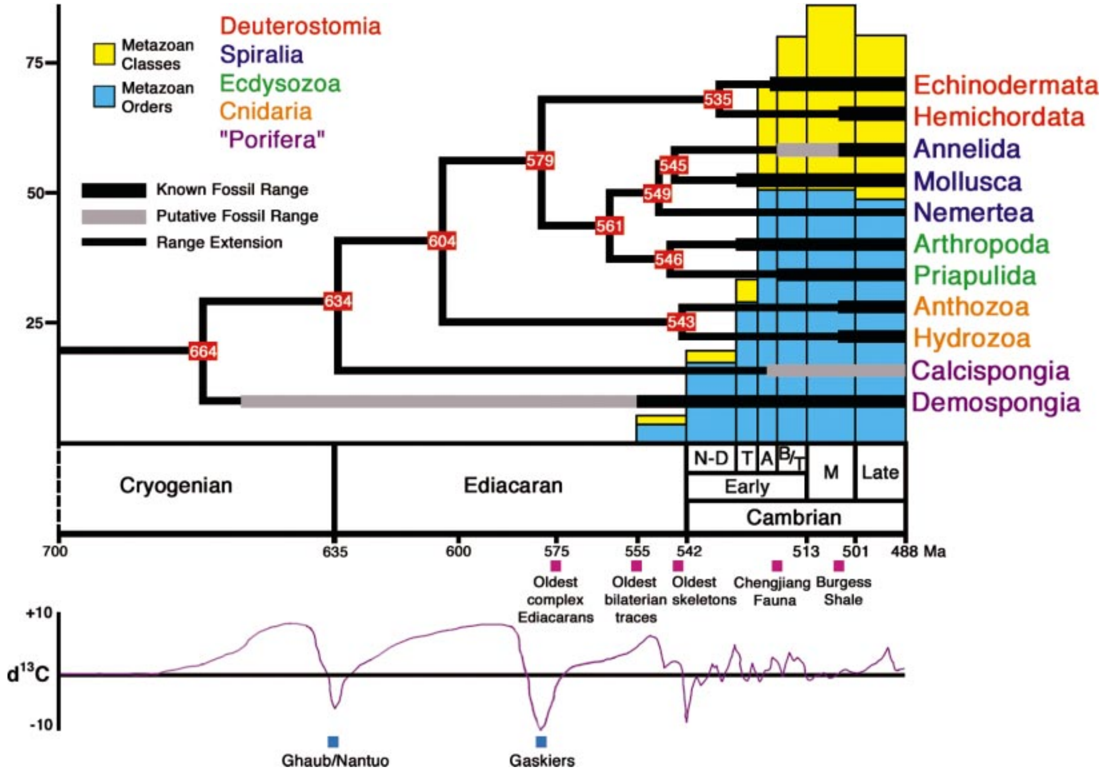

FIGURE 2. Tempo of early animal evolution placed into the geologic context of the Neoproterozoic/Cambrian transition. Tree nodes are positioned according to the updated molecular clock estimates of Peterson et al. (2004; Peterson unpublished). The generalized Precambrian carbon isotope curve is from Knoll 2000. Boundary ages are from the 2003 ICS International Stratigraphic Chart except for the Cryogenian/Ediacaran boundary (Knoll et al. 2004), which is placed at 635 Ma on the basis of Hoffman et al. 2004 and Condon et al. 2005. Note that according to Calver et al. (2004) this boundary could be as young as 580 Ma and thus the Marinoan and Gaskiers glaciations could be synchronous; see the text for further discussion. All other ages are listed in Table 1. Abbreviations: N-D; Nemakit-Daldynian; T; Tommotian; A; Atdabanian; B/T; Botomian/Toyonian; M; Middle. (Adapted from Knoll and Carroll 1999.)

istence of significant rate heterogeneity associated with the vertebrate sequences when compared with most invertebrate sequences (see also Ayala et al. 1998). Indeed, Peterson et al. (2004) showed that the rate of molecular evolution decreased in vertebrates about twofold with respect to three different invertebrate lineages (echinoderms, bivalves, and insects). This is significant because vertebrates are usually used to calibrate the molecular clock, and thus a twofold decrease in the rate of vertebrate sequence evolution causes about a two-fold overestimate of the vertebrate-dipteran divergence (see also Benton and Ayala 2003). Studies that either exclude vertebrates (Peterson et al. 2004) or allow substitution rates to vary among taxa (Aris-Brosou and Yang 2002, 2003) give estimates much closer to the those derived from a synoptic reading of the fossil record (Fig. 2).

In addition, Peterson et al. (2004) and Peterson (unpublished) tested the accuracy of their clock by estimating a divergence when both a minimum and a maximum are known from the fossil record. The minimum age for the split between crinozoan and eleutherozoan echinoderms is 485 Ma (Landing et al. 2000) and is derived from the first occurrence of unequivocal crown-group echinoderms (stem-group crinoids from the Tremadocian [Guensburg and Sprinkle 2001]). The maximum age is 525 Ma (Landing et al. 1998) and is derived from the first occurrence of stereom in the fossil record (stem-group echinoderms from the

TABLE 1. High-precision ages from late Neoproterozoic stratified successions.

Location	Formation (Group)	Age (Ma)	Relation to stratigraphically important events	Ref.
Terminal Proterozoic cratonic successions				
Oman	(Ara)	542 ± 0	Ediacaran/Cambrian boundary $(-)\delta^{13}$C excursion	1
Namibia	Urusis	543 ± 1	Immediately below Cambrian; Cloudina	2
Oman	Fara (Ara)	545 ± 3	Immediately below Cambrian	3
Namibia	Zaris	549 ± 1	$(+)\delta^{13}$ C excursion; diverse Ediacara fossils	2
Poland	(Volhyn)	551 ± 4	In borehole 200 m above diamictite	4
White Sea	Ust-Pinega	555 ± 0	*Kimberella*-bearing assemblage	5
Avalonian-Cadomian arc				
England	Beacon Hill	559 ± 2	Immediately underlies Ediacara-bearing strata	6
Newfound.	Mistaken Point	565 ± 3	Diverse frondose Ediacara assemblage	7*
Newfound.	Drook	ca. 575	Simple frondose Ediacara assemblage	8*
Newfound.	Gaskiers	ca. 580	Ashes below, within, and above glaciogenic unit	8*
NE U.S.A.	Mattapan	595 ± 2	Older than Squantum glaciogenic deposit	9
Laurentian late-stage rifts				
SW Canada	(Hamill/Gog)	570 ± 5	Above marker dolostone = Icebrook cap equiv?	10
E U.S.A.	(Catoctin)	ca. 570	Closely associated with Fauquier Gp diamictite	11
Scotland	Tayvallich	601 ± 4	12 km above Port Askaig ''Tillite''	12
Proto-Gondwanaland terminal Proterozoic successions				
Tasmania	(Grassy)	ca. 580	Pre-(?) and postglacial volcanic rocks	13
S China	Doushantuo	551 ± 1	Minimum age for metazoan embryos	14
		635 ± 1	Ash bed within post-Nantuo cap carbonate	14
N Namibia	Ghaub	636 ± 1	Ash bed within glaciogenic formation	15
S Australia	Marino	ca. 650	Two detrital zircons in arkose below Elatina level	16
S China	Datangpo	663 ± 4	Older than the Nantuo glaciogenic deposit	17

References: (1) Amthor et al. 2003; (2) Grotzinger et al. 1995; (3) Brasier et al. 2000; (4) Compston et al. 1995; (5) Martin et al. 2000; (6) Compston et al. 2002; (7) Benus 1988; (8) Bowring et al. 2003; Narbonne and Gehling 2003; (9) Thompson and Bowring 2000; (10) Colpron et al. 2002; (11) Aleinikoff et al. 1995; (12) Dempster et al. 2002; (13) Calver et al. 2004; (14) Condon et al. 2005; (15) Hoffmann et al. 2004; (16) Ireland et al. 1998; (17) Zhou et al. 2004.

* Age not fully published with analytical data.

Nevadella trilobite zone [Smith 1988]). Peterson et al. (2004) estimated this divergence at 508 Ma, well within the range of dates established by the fossil record. The second point is the divergence between the vetigastropod *Haliotis* and the sorbeconch *Crepidula*, which the fossil record estimates at 501–488 Ma (Lindberg and Guralnick 2003) and the molecular clock estimates at 500 Ma (Peterson unpublished). These two checks suggest that the molecular-clock estimates summarized here are accurate.

Summary.—The most recent clock studies, coupled with a new understanding of metazoan relationships and precise geochronological tie points, estimate that many different lineages of triploblastic ''worms'' crawled across the boundary, in addition to the other extant metazoan lineages that were present in the Ediacaran (calcisponges, silicisponges, ctenophores, and cnidarians). Thus, the Ediacaran/Cambrian boundary seems to correspond to the time when many metazoan phylum- and class-level divergences were occurring (Fig. 2). Hence, the cladogenic events underlying the origin of modern phylum-level lineages and the gradual acquisition of each of the phylum-level body plans would seem to go hand in hand: Unique bilaterian body plans evolved in the context of a diversification event that started around 600 Ma and culminated with the phylum-level splits around 540 Ma, dates consistent with the known fossil record of metazoans (Xiao et al. 1998; Budd and Jensen 2000; Jensen 2003; Condon et al. 2005), and with the Proterozoic fossil record in general (Butterfield 2004).

Hox: Internal Trigger(s)

> The question of one vs. ten [''worms'' crawling across the Precambrian/Cambrian boundary] does, however, bear strongly upon the important question of internal vs. external triggers for the explosion. If only one lineage generated all Cambrian diversity, then an internal trigger based upon some genetic or developmental ''invention'' becomes plausible. (Gould 2002)

Our thesis below is that the spectacular radiation of animals during the late Precambrian and early Cambrian was inevitable once macrophagous predators evolved near the end of the Neoproterozoic. For the first time in earth history, predation pressures drove macroevolution of not just animals, but other eukaryotic lineages as well. Hence, understanding how and why bilaterians achieved macroscopic size within a few tens of millions of years after their origination at ca. 600 Ma is the first key to unraveling the mystery of the Cambrian explosion.

Macrophagy and the Cambrian Explosion.—The first two essays Gould wrote on the Cambrian explosion were a perspective on Stanley's (1973) paper on cropping (Gould 1979a: pp. 126–133), and an argument that the explosion itself follows a general law of growth (Gould 1979: 119–125). Both essays convey the general idea that the Cambrian explosion was inevitable: ''Perhaps the explosion itself was merely the predictable outcome of a process inexorably set in motion by an earlier Precambrian event'' (Gould 1979). We agree with this view and contend that the Cambrian explosion is the paleontological manifestation of the evolution of predation, specifically the origin of and defense against macrophagy, within the phylogenetic context of the bilaterian radiation.

Ignoring the highly unusual form of macrophagy found in cladorhizid sponges (Vacelet and Boury-Esnault 1995), macrophagy is a derived state within Metazoa because the paraphyly of sponges (Fig. 1) implies that the last common ancestor of metazoans, and also calcareous sponges + eumetazoans, had a water-canal system, and thus must have fed intracellularly on free organic matter and demersal bacteria, as both groups of sponges still do today (Brusca and Brusca 2002). This reliance upon intracellular digestion restricts the upper limit of their prey size to approximately 5 μm (Brusca and Brusca 2002), which excludes most forms of eukaryotic phytoplankton and, of course, other animals as prey items. Thus, planktonic eukaryotic algae would have been invulnerable to metazoan predators during this time interval, and, not surprisingly, acritarch taxa are morphologically monotonous from ca. 2 Ga until just after the 653 Ma Nanto glacial deposit (Butterfield 1997; Peterson and Butterfield unpublished), a morphology characteristic of phytoplankton that do not experience herbivory (Reynolds 1984; Sommer et al. 1984; Leibold 1989).

Macrophagy must have evolved at the base of Eumetazoa because all three major groups—ctenophores, cnidarians, and triploblasts—each have a mouth and a functional gut to digest food extracellularly. None use a water-canal system, which was lost by the time eumetazoans arose, and thus no necessary restrictions of prey size like that of sponges would exist. We hypothesize that benthic grazing is the primitive mode of feeding for eumetazoans, which means that these animals should have been able to feed upon anything living in the bacterial mats that was smaller than themselves, including bacteria, algae, and presumably other animals.

Bearing in mind the obvious taphonomic window through which we view the Burgess Shale biota (Butterfield 2003), this hypothesis does conform to the known distribution of feeding modes such that an overwhelming majority of the described Cambrian eumetazoans are epifaunal or infaunal vagrants, dominated by arthropods and priapulids, respectively (Conway Morris 1979, 1986). In contrast, the epifaunal suspension feeders are primarily sponges, with only brachiopods and a few echinoderms and other enigmatic forms (e.g., *Dinomischus*) feeding upon eukaryotic plankton (see also Signor and Vermeij 1994). Nonetheless, the trophic mode of both cnidarians and ctenophores, as well as ecological considerations of Ediacara assemblages (e.g., Conway Morris 1986; Clapham and Narbonne 2002; Clapham et al. 2003), would seem to suggest that suspension feeding is primitive for Eumetazoa. However, whether or not Ediacaran organisms were metazoans is a contentious issue, and several recent treatments find more similarities with modern fungi than with modern animals (Steiner and Reitner 2001; Peterson et al. 2003). More importantly, the fractal design of many Ediacara organisms (Narbonne 2004) and the lack of any obvious openings, coupled with their ecological tiering (Clapham and Narbonne 2002; Clapham et al. 2003), suggest that they could only feed on dissolved organic manner in a unique fashion when compared with either sponges or eumetazoans, irrespective of their actual phylogenetic position, and thus are irrelevant for polarization.

Suspension feeding is unlikely to be primitive for cnidarians because the earliest cnidarians could not have yet evolved nematocysts. We hypothesize that the earliest cnidarians grazed upon benthic organisms in a manner similar to that of triploblasts. Indeed, it may be better to think about cnidarians as originating from acoelomorph-like animals, as opposed to acoelomorph-like animals evolving from planula larva (e.g., Jondelius et al. 2002), especially given the presence of both an anterior/posterior and a cryptic dorsal/ventral axis in anthozoans (Hayward et al. 2002; Finnerty et al. 2004). The evolution of cnidarian polyps with nematocyst-laden tentacles could only have occurred after the evolution of an appropriate food source, namely mesozooplankton, which is probably no older than about ca. 560 Ma (Peterson unpublished). Given that total-group Cnidaria originated ca. 600 Ma, there must have been stem-group cnidarians that fed on other food sources. With respect to ctenophores, not only are their colloblast-laden tentacles of unique construction (Brusca and Brusca 2002), but they are also absent from all known Cambrian ctenophores (Conway Morris and Collins 1996; Chen and Zhou 1997), making suspension feeding a derived condition here as well.

The Evolution of Complex Life Cycles.—The evolution of complex life cycles is coupled with the relative size increase in animals in response to predation. The idea that direct development with a benthic adult stage is primitive for Triploblastica contrasts sharply with the hypotheses of Nielsen (1998) and Peterson et al. (2000), who suggested that the earliest triploblasts were ciliated planktotrophic larval-like forms. This hypothesis is problematic for numerous reasons (see also Conway Morris 1998; Budd and Jensen 2000; Valentine and Collins 2000; Sly et al. 2003). First, as discussed above, the basal position of acoels suggests that the primitive condition for Triploblastica is a uniphasic life cycle that lacks a pelagic larval stage (Baguñà et al. 2001; Jondelius et al. 2002). Second, most metazoan phyla, including triploblasts, are adapted to live on the benthos, not in the pelagos (Valentine et al. 1999; Collins and Valentine 2001). Third, the paraphyly of Porifera (Fig. 1), and the primitiveness of the cnidarian polyp stage (e.g., Bridge et al. 1995; Collins 2002), implies that the last common ancestor of metazoans, the last common ancestor of calcisponges and eumetazoans, and the last common ancestor of bilaterians all had an obligate benthic adult stage. Fourth, the general direction of evolution among both metazoans and non-metazoans is from the benthos to the pelagos and not the reverse (Rigby and Milsom 1996, 2000). Fifth, because internal fertilization is primitive for both Triploblastica and Nephrozoa (Buckland-Nicks and Scheltema 1995), small size combined with direct development is most likely primitive as well (Olive 1985; Chaffee and Lindberg 1986). Finally, the known fossil record suggests that the benthos is the primitive site of animal evolution given that the earliest known bilaterian macrofossil, *Kimberella*, is a benthic animal (Fedonkin and Waggoner 1997), and pelagic forms are extremely rare, if present at all, in the Ediacara biotas (Fedonkin 2003). Therefore, pelagic larvae are not primitive; instead larvae were independently intercalated into an existing direct-developing strategy (Sly et al. 2003) multiple times (Hadfield 2000; Hadfield et al. 2001).

This convergent evolution of maximal indirect development (Davidson et al. 1995) from direct development is difficult to understand because in the modern world larvae offer few, if any, evolutionary advantages (Pechenik 1999). In addition, natural selection should not favor the lengthening of a pre-adult stage or the addition of pre-adult stages; selection should predominantly favor the evolution of rapid development (Williams 1966). To us, the independent evolution of larvae, as well as other forms of mesozooplankton, is a solution to an ecological problem, namely the problem of benthic predation (Signor and Vermeij 1994). This hypothesis is consistent with four key features of the evolutionary history of the rise of larvae themselves. First, the evolution of positive phototaxy and locomotive ciliary bands allow for negatively buoyant eggs and embryos to stay within the pelagos and away from the predator-rich benthos (Pechenik 1979). Second, benthic predation would have disproportionately affected the smallest size classes of each species; this accounts for the migration of eggs and initial free-living forms into the pelagic zone first, instead of older, and thus larger, life stages, which occurred in a few cases later in geological time (Rigby and Milsom 1996, 2000). Third, the rise of larvae is not due solely to the exploitation of novel resources (e.g., phytoplankton) because phylogenetic considerations suggest that the many of the earliest larval forms were non-feeding (McHugh and Rouse 1998; Rouse 2000). And fourth, predation pressures from macrozooplankton (e.g., cnidarian medusae, ctenophores, chaetognaths, and vertebrates [Young and Chia 1987]) was virtually nonexistent until the late Early Cambrian (Vannier and Chen 2000). In addition, although some larval forms show macroevolutionary responses to predation (Nützel and Fryda 2003), even today, thanks to their small size and optical clarity, larvae are not heavily preyed upon (Johnson and Shanks 2003). Hence, planktonic predation pressures have played a minor role in the evolution of larvae, consistent with the relatively long periods they spend in the pelagos.

Benthic predation pressures may have also selected for the evolution of ''set-aside'' cells (Davidson et al. 1995; Peterson et al. 1997). It appears that the principal function of a larval stage is not dispersal, but growth (Strathmann 1987, 1993). Growth is of fundamental importance because benthic suspension feeders ingest particles within a size range that includes most marine larval forms (Young and Chia 1987), and thus larvae cannot escape predation until they have grown larger than their typical size at metamorphosis (Pechenik 1999). Therefore, benthic predation pressures would select for the rapid growth of juveniles. Rapid growth on the benthos independent of juvenile feeding requires that much of the juvenile body plan already be ''prepackaged'' within the larvae; this could be accomplished if larvae began adult body plan construction while still in the plankton. Consistent with prediction, then (Williams 1966), the evolution of set-aside cells makes obvious ecological and evolutionary sense: they allow for maximal growth (Strathmann 1987; Hadfield 2000) during the time of maximal predation (MacGinitie 1934) and thus are a convergent solution to a ubiquitous problem (Bishop and Brandhorst 2003; Sly et al. 2003).

Molecular Control of Body Size.—The independent evolution of both coeloms and larvae strongly suggests that the direction of nephrozoan evolution was from small direct-developing acoelomates to large indirectly developing coelomates, and not the reverse. Consistent with this hypothesis, the dearth of body fossils and, more importantly, trace fossils before 555 Ma (Martin et al. 2000; Jensen 2003) suggests that the earliest nephrozoans were under 1 cm, and probably closer to 1 mm, in length (Erwin and Davidson 2002). This predicts, then, that the evolutionary increase in body size (or, more appropriately, mass [see Conlon and Raff 1999]), occurred numerous times independently. Growth is regulated by both extrinsic and intrinsic inputs that are linked in an unknown manner (Johnston and Gallant 2002) and must work at the appropriate scale (Nijhout 2003). These inputs can be classified into three types: (1) growth factors that stimulate protein synthesis, resulting in an increase in cell size; (2) mitogens that increase cell number by stimulating cell division; and (3) survival factors that prevent programmed cell death (Conlon and Raff 1999). These inputs are primitive for at least Bilateria, because an insulin receptor was characterized from the cnidarian *Hydra* (Steele et al. 1996) and the mitogen *myc* appears in the *Hydra* EST database (CN550970).

Importantly, defects in the mitogen pathway result in a smaller body size in both flies and mice, but the pattern of the body plan appears unaffected (Trumpp et al. 2001). Hence, interrelated with growth is the ability to pattern groups of cells during development (Davidson et al. 1995). Pattern formation, as defined by Davidson et al. (1995), consists of the regulatory processes required to partition undifferentiated regions of an embryo into areas of specific morphogenetic fate, and it is the depth of the gene regulatory networks responsible for pattern formation that delays the specification of cells and thereby allows for growth (Davidson 2001). Arguably the best-known pattern formation genes are the Hox genes, which play a crucial role in controlling cell proliferation in a position-dependent manner (Duboule 1995). Although a link between Hox genes and proliferation was apparent from studies on carcinomas (Carè et al. 1996; Naora et al. 2001; see Abate-Shen 2002 for review), it was not apparent how a developmental regulatory gene interacts with the cell cycle. Recently, Luo et al. (2004) showed that one link is the protein geminin. Geminin controls cell replication by interacting with an essential component of the replication complex, Cdt1: binding with Cdt1 inhibits DNA replication and hence cell division, whereas the degradation of geminin allows Cdt1 to assemble with several other proteins and results in replication initiation, and ultimately cell proliferation (Li and Rosenfeld 2004). Luo et al. (2004) also demonstrated that geminin interacts with Hox genes as well, which displaces it from Cdt1 and thus promotes cell division. In addition, geminin can antagonize Hox gene function by displacing it from target sites of downstream genes. Therefore, important developmental regulators can control the cell cycle by preventing DNA replication, and a cell cycle regulator can affect development by inhibiting the DNA binding of transcription factors, and all of this can be mediated by the competitive regulation of a single protein.

Using the presence of a Hox complex as a proxy for the evolution of pattern formation suggests that pattern formation is primitive for at least Bilateria, given that the planula stage of the anthozoan *Nematostella* expresses Hox genes in a colinear manner along the oral-aboral axis of the larva (Finnerty et al. 2004). Curiously, to date no authentic Hox genes have been reported from ctenophores or sponges (Martindale et al. 2002) despite the presence of MetaHox genes such as *Tlx, NK2,* and *Msx* in sponges (Coutinho et al. 2003), which were primitively linked to Hox genes in a ''MegaHox'' cluster (Coulier et al. 2000; Pollard and Holland 2000; Holland 2001). Whether this means that the tandem duplications that gave rise to Hox genes from a MetaHox gene had not yet occurred, or instead that sponges lost all Hox genes, or simply that they are not easily amplified under standard PCR conditions, is unknown and will remain so at least until a sponge genome is sequenced. Nonetheless, their apparent absence in ctenophores as well suggests that pattern formation, as assessed by a cluster of collinearly expressed Hox genes, is restricted to bilaterians, and might be the innovation largely responsible for the rapid diversification of the bewildering array of bilaterian body plans during the late Precambrian and Early Cambrian (Davidson et al. 1995).

Summary.—All available data suggest that the earliest eumetazoans were direct developing, micrometazoan benthic predators (e.g., Boaden 1989; Fortey et al. 1996, 1997; Jondelius et al. 2002; Valentine and Collins 2000; Sly et al. 2003). The invention of pattern formation as a form of growth control during development is the key innovation that ultimately allowed for the evolution of macroscopic bilaterian body plans during the Ediacaran Period, and it is our contention that the evolution of macrophagy is what drove this increase in body size. It is inevitable, then, that large, indirectly developing skeletonized animals would appear within a few million years after the evolution of macrophagy, and it is no surprise that the first appearances of skeletons at 545 Ma (Amthor et al. 2003) follow, rather than precede, the large, but simple, traces first recorded at 555 Ma (Martin et al. 2000), as predicted by Stanley (1976a,b).

Rocks: External Trigger(s)

> But . . . the transformation of ten tiny worms into the larger and well differentiated *Baupläne* of Cambrian phyla suggests an external trigger . . . [and] the melting of a ''snowball earth'' sometime before the Cambrian transition may well represent [a] plausible environmental trigger. (Gould 2002)

Thus far, we have argued that the critical temporal window for understanding early bilaterian evolution is between 650 and 550 Ma. Furthermore, we identified a potential candidate for an ''internal trigger'' necessary for the rapid rise of macrophagic predators by the late Early Cambrian, namely pattern formation processes (Davidson et al. 1995). Of course, one cannot divorce genetic innovations from the environmental problems those innovations are developed to solve, and there is no lack of dramatic, global environmental changes in the terminal Neoproterozoic interval. In addition to the possibility that our planet was engulfed in ice for 5–10 million years at a time, perhaps several times during the latter half of the Neoproterozoic Era (Hoffman et al. 1998), one of the largest recognized bolide impact events in the entire geological record occurred within this same time period as well (Grey et al. 2003; Williams and Wallace 2003). Furthermore, paleomagnetic data suggest very rapid changes in global paleogeography, possibly involving episodes of true polar wander (e.g., Kirschvink et al. 1997; Evans 2003), and there appears to have been a significant increase in the oxidation state of the ocean system (Knoll 2003). The following discussion considers the evolutionary consequences of ''snowball Earth'' and the rise of atmospheric oxygen, because these two factors can be most easily implicated in generating high-level taxonomic innovations, although clearly a catastrophic impact and dramatic changes in ocean circulation must have had some effect upon Earth's late Precambrian and Cambrian biota as well (e.g., Kirschvink and Raub 2003).

Snowball Earth.—Distinctive hallmarks of glaciation pepper the late Neoproterozoic stratigraphic record of nearly every craton, among all present continents. Direct juxtapositions of glaciogenic diamictites with carbonate rocks, as well as numerous paleomagnetic data indicating near-equatorial paleolatitudes of deposition (reviewed by Evans 2000), suggest that the Neoproterozoic ice ages were global affairs (reviewed by Hoffman and Schrag 2002). Direct age constraints on glaciogenic deposits have only recently begun to provide precise relationships between the number of glaciations and the deduced timing of metazoan divergences as assessed by the molecular clock (see above). The number of Neoproterozoic ice ages has been considered to be as few as two and as many as five (e.g., Kaufman et al. 1997; Kennedy et al. 1998; Evans 2000; Hoffman and Schrag 2002), but this paper will simplify the debate by discussing only those with likely ages younger than 650 Ma, and thus relevant with respect to bilaterian evolution as assessed by the molecular clock (Fig. 2).

Of particular relevance for this discussion is the age of the true Marinoan glaciation interval, that is, defined by rocks of the near-equatorial Elatina Formation (Sohl et al. 1999, and references therein) and correlative units within the Marinoan chronostratigraphic series that is restricted to Australia. This ice age occurred between ca. 650 and 580 Ma, according to detrital zircons from an underlying arkose in South Australia and igneous zircons from subsequent volcanism on King Island, Tasmania (Ireland et al. 1998; Calver et al. 2004). It is important to emphasize the exact age constraints on this particular group of deposits, free of extrabasinal correlations, because they show the best evidence for deep tropical paleolatitudes (reviewed by Evans 2000)—other paleomagnetic determinations of tropical glaciogenic deposits (e.g., Macouin et al. 2004) suffer from the absence of tightly constrained field stability tests that are needed to prove a primary origin of the magnetizations. However, several non-Australian deposits that are generally correlated to the Marinoan ice age are directly dated at 635 Ma in central Namibia (Hoffmann et al. 2004) and South China (Condon et al. 2005).

Glaciogenic rocks of the Gaskiers Formation, in Newfoundland, are constrained to an age of 580 Ma (Bowring et al. 2003). However, it is uncertain whether the Gaskiers and related units in the Avalonian-Cadomian volcanic arc (Thompson and Bowring 2000) correlate with the Marinoan ice age, or if they instead represent a younger glaciation of merely regional extent (see Myrow and Kaufman 1999; Evans 2000; Xiao et al. 2004; Condon et al. 2005). Regardless of the specific correlations, most of the world's youngest Proterozoic glaciogenic deposits can be grouped into two episodes, dated at 635 and 580 Ma.

In addition to the uncertainty surrounding both the number of glacial episodes and their absolute ages, the effort to characterize a snowball event stretches the notion of climate change to the limits of imagination. The most complete model thus far advanced includes a ''freeze-fry'' scenario of extreme warming following the buildup of greenhouse gases needed to escape the snowball state (Hoffman et al. 1998; but see Pierrehumbert 2004). Syn-snowball accumulation of those greenhouse gases (mainly CO_2) would have been achieved via volcanic outgassing and highly attenuated chemical weathering of silicate rocks, the atmosphere's major long-term (and strongly temperature-dependent) CO_2 sink (Walker et al. 1981; Kirschvink 1992). A more conservative view of the Neoproterozoic ice ages in terms of Pleistocene-like glacial-interglacial cycles, but with recognition that the deposits encroached deep within the Tropics, has been dubbed the ''slushball'' model. Although supported by the glacial-interglacial sedimentary sequences (Condon et al. 2002; Leather et al. 2002), and some numerical climate models (e.g., Hyde et al. 2000), this perspective cannot explain the reappearance of banded-iron formations and the existence of cap carbonates with their ubiquitous carbon-isotopic excursions (Schrag and Hoffman 2001).

Each model hypothesizes different effects upon the biota. Biological refugia within a ''slushball'' ice age are easy to imagine given that the deep Tropics would have included vast expanses of open seawater (Hyde et al. 2000). Full-blown snowball ice ages would harbor more subtle refugia. Submarine hydrothermal vents at the mid-ocean ridges would provide a continuous source of energy and nutrients throughout the glaciation, permitting survival of that ecosystem at nearly modern conditions. Within the ice, ablation from the surface would be balanced by a continuous flux of basal freezing to maintain steady-state thickness (modified by equatorward flow; see below). In this way, nutrients such as hydrothermal iron could reach the photic zone where bacteria, algae, and metazoans could survive within brine cavities. Above the ice, long-lived continental volcanic fields could maintain hydrothermal systems for thermophilic microbes throughout the cold spell. Recent considerations of marine ice dynamics, which indicate maintenance of super-equilibrium thickness in the Tropics due to ocean-scale sea glacier flow from high latitudes (Goodman and Pierrehumbert 2004), suggest that large regions of the tropical ocean could have remained ice covered even while the ice within more protected embayments melted away as greenhouse gases accumulated over the course of several million years. Such a process would create several geographically isolated regions of warm seawater enduring throughout the late stages of a prolonged snowball regime (Halverson et al. 2004).

In sum, as long as microbes and primitive metazoans could find a refuge during the early stages of a snowball episode, then the waning stages could foster evolutionary innovation among small populations of survivors within several geographically distinct regions. Given that a widespread Marinoan glaciation occurred at 635 Ma (Hoffman et al. 2004; Condon et al. 2005), then our estimate of the origin of eumetazoans somewhere between 634 and 604 Ma could have occurred on the heels of snowball Earth. In addition, at least five lineages of living animals (silicisponges, calcisponges, ctenophores, cnidarians, and triploblasts) must have survived the Gaskiers ice age (Fig. 2), casting doubt on the global import of this glaciation. Alternatively, if the definitively low-latitude Marinoan glaciation is as young as 580 Ma (Calver et al. 2004), then a much more severe environmental perturbation is implied, but one may question how it could be possible for these five animal lineages to withstand a ''hard'' snowball ice age (Hoffman et al. 1998) given the plethora of feeding modes and reproductive strategies these animals utilize. Thus, the phylogenetic constraint derived from molecular-clock analyses could aid our perceptions of a snowball world and shed deeper insight into its impact upon the biota, once the number of episodes, their absolute ages, and their paleogeographic distributions are better characterized.

Oxygen.—Suggestions that rising oxygen levels permitted bilaterians to attain large size have been voiced for nearly 50 years (reviewed in Knoll and Carroll 1999; Knoll 2003). Independent evidence for an increase in atmospheric oxygen concentration during the terminal Proterozoic to Cambrian interval comes from carbon and sulfur isotope records, which suggest that oxygen levels increased dramatically after the Sturtian interval (Fig. 2). Importantly, this rise in oxygen cannot explain the origin of large bilaterians, because the relative levels necessary for increased size and complexity of eukaryotes was already in place (Canfield and Teske 1996) before 570 Ma (Colpron et al. 2002).

Nonetheless, the distribution of oxygen in the water column might have played a fundamental role in the evolutionary history of bilaterians. On the basis of stable carbon isotopes of molecular biomarkers, Logan et al. (1995) proposed that the nearly complete (sulfate-reducing) bacterial degradation of primary algal products inhibited the transport of oxygen into the deep Proterozoic ocean. This stands in contrast to Phanerozoic geochemical cycling, whereby fecal-pellet transport of reduced carbon to the deep benthos limits midwater sulfate reduction, and thus oxygenates the benthos. This model predicts that Proterozoic oceans should have been more redox-stratified than at present and is supported by isotopic data from ^{13}C (Shields et al. 1997) and ^{34}S (Shen et al. 2003) across Proterozoic paleodepth gradients. Hence, the continued increase in size of benthic animals would depend upon the increase in oxygenation provided by the carbon flux from the pelagos. Although this model provides an attractive link between our model of zooplankton evolution and the subsequent appearance of large metazoan body fossils, the utility of the biomarker stable-isotope proxy for dating the onset of fecal-pellet generation by zooplankton depends on the age constraints of the sampled sedimentary rocks, which at the moment can only be constrained to between the Early Cambrian and the late Neoproterozoic (Schaefer and Burgess 2003).

Summary.—Poor numerical age control of late Neoproterozoic sedimentary successions is presently the major hindrance to unraveling the web of conceivable external influences on early metazoan evolution. As determined by a variety of measurements, the terminal Proterozoic interval was clearly a time of Earth-system agitation. If further geochronology constrains the definitively low-latitude glaciogenic strata to 635 Ma, global glaciation could have been a driving factor in the origin and subsequent evolution of eumetazoans by giving ample opportunity for an extinction and subsequent ecological recovery event (e.g., Hoffman et al. 1998; Hoffman and Schrag 2000; Narbonne and Gehling 2003). In addition, the oxygenation of the benthos via reduced carbon derived from fecal pellets would have allowed for the evolution of increased size, a necessary cofactor for the successful evolution of indirectly developing life cycles (Olive 1985).

Internal and External Triggers: Putting It All Together

> The Cambrian explosion still requires a[n external] trigger . . . but our understanding of the geological rapidity of this most puzzling and portentous event in the evolution of animals will certainly be facilitated if the developmental prerequisites already existed in an ancestral taxon. (Gould 2002)

A key insight into the nature of the Cambrian explosion was made by Butterfield (1997): The ecological ramifications resulting from the invasion of small animals into the plankton to avoid benthic predation (Signor and Vermeij 1994) changed the pelagos from a single trophic to a multitiered ecosystem (Stanley 1973, 1976a,b). The effect of evolving mesozooplankton by ca. 510 Ma (Butterfield 1994), but possibly earlier (see above), would have been immediate, with pelagic algae evolving antipredator defenses by the early Cambrian (Butterfield 1997, 2001); such structures would have come at a cost given that, at least among modern prey, spines and other antipredatory devices are quickly lost when the predator is removed from the system (Sommer et al. 1984; Leibold 1989; Reynolds 1984). Furthermore, the advent of planktic skeletons by the end of the Cambrian (e.g., Tolmacheva et al. 2001; Pawlowski et al. 2003), in response to mesozooplankton predation pressures (and this in response to benthic predation pressures), not only changed the potential for future global glacial episodes (Ridgwell et al. 2003), but also severely reduced the potential for subsequent Burgess Shale-type deposits (Gaines 2003). Thus, the window through which Stephen Jay Gould discerned patterns and processes in early animal evolution (Gould 1989) was both created and destroyed by the same causal factors: the advent of pelagic multi-tiered food webs constructed on the heels of snowball Earth.

The evolution of mesozooplankton would have had another very important effect; they would have served as a food source for macrozooplankton and nekton, and it is their evolution that would have changed the oxygenation potential of the benthos and thus increased benthic productivity. As mentioned above, the dramatic reorganization of biogeochemical cycles that occurred sometime between the latest Neoproterozoic and Early Cambrian (Logan et al. 1995) is attributed to the evolution of pelagic metazoans whose fecal pellets would remove organic matter from the pelagos and deliver it to the benthos. Importantly, the fecal pellets of meso- and microzooplankton make little or no contribution to the sedimentary flux (Butterfield 1997; Turner 2002), and, if anything, their evolution would have decreased the amount of organic rain to the benthos as the fecal pellets of small metazoans were processed within the water column. However, the fecal pellets of macrozooplankton and nekton are large enough to settle before they are consumed in the pelagos (Turner 2002). The evolution of macrozooplankton and nekton sometime around the Precambrian/Cambrian boundary, as deduced by the data of Logan et al. (1995), is consistent with the maximal date of 543 Ma for the evolution of the cnidarian medusae as estimated by the molecular clock (Fig. 2), and the 520 Ma date for bona fide fossil macrozooplankton and nekton (Chen and Zhou 1997; Vannier and Chen 2000).

The evolutionary ramifications of mesozooplankton are not limited to the pelagos, as they strongly affected the subsequent evolution of the animals on the benthos as well, given that pelagic predators evolved from benthic ancestors to take advantage of this new and very plentiful food source, and also that benthic suspension-feeding predators evolved to capitalize on these new prey. Thus, the evolution of mesozooplankton links the eukaryotic plankton to the eukaryotic benthos and effectively establishes the ''modern'' or Phanerozoic ocean (Butterfield 1997). But like large size and skeletons, the evolution of mesozooplankton is itself a response to benthic predation, and hence it is the evolution of eumetazoans themselves as mobile multicellular heterotrophs near the end of the Cryogenian—possibly in response to a selective event involving global perturbations and mass extinctions—that was the ultimate cause of the Cambrian explosion, as their spectacular radiation, and the radiations of their prey (and predators) were inevitable once these animals evolved pattern formation processes. Although not by any means the last word on the subject, it is our sincere hope that the ideas presented in this paper, inspired by the perspicacious writings of Stephen Jay Gould, have brought our understanding of this singular episode in the evolutionary history of animals a bit closer in reach.

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