so that structure and constraint, the formerly disfavored and neglected first terms of each pairing, can achieve the same attention and respect that we properly accord to the proven potency of Darwinian forces represented by the second term in each pairing.

SETTING OF HISTORICAL CONSTRAINTS IN THE CAMBRIAN EXPLO-SION. Hughes (2000, p. 65) has expressed this cardinal discovery of evo-devo in phyletic and paleontological terms: "It is hard to escape the suspicion that what we witness in the Cambrian is mainly tinkering with developmental systems already firmly established by the time these Cambrian beasts showed up." As a reminder for non-paleontologists, all major bilaterian phyla with conspicuously fossilizable hard parts make their first appearance in the fossil record within the remarkably short interval (5–10 million years, but probably near or below the lower value) of the so-called Cambrian explosion (535–525 million years ago). (The single exception, the Bryozoa, first appear in the subsequent Ordovician Period.)

Unfortunately, however, as the data of molecular phylogeny accumulate, a conceptual error has begun to permeate the field, and to stymie the integration of this new source with direct information from the fossil record of early animal life, a field that has also enjoyed a renaissance in both methodology and discovery during the past twenty years (Gould, 1989c; Conway Morris, 1998; Knoll and Carroll, 1999). Although some molecular estimates for the divergence times of animal phyla correspond closely with the Cambrian explosion itself—Ayala et al. (1998), for example, cite 670 million years for the chordate vs. echinoderm division within deuterostomes—the majority of sources posit a much earlier set of divisions, deeply within Precambrian times. Wray et al. (1996) give 1.2 billion for protostomes vs. deuterostomes, and 1.0 billion for echinoderms vs. chordates; while Bromham et al. (1998) calculate confidence intervals broadly consistent with Wray et al.'s earlier dates. The 680 million year upper bound of their intervals (with much older means, of course) still suggests a minimal splitting age at least 150 million years before the explosion itself.

I do not possess the requisite skills to evaluate these different estimates, and the current literature seems too labile for a confident conclusion in any case. But I can assert that proponents of the older dates have muddied conceptual waters by supposing that their deeply Precambrian splitting times somehow either invalidate, or at least strongly compromise, the reality of the Cambrian explosion. For example, Wray et al. (1996) write: "Our results cast doubt on the prevailing notion that the animal phyla diverged explosively during the Cambrian or late Vendian, and instead suggest that there was an extended period of divergence . . . commencing about a billion years ago."

Bromham et al. (1998) codify this fallacy by inventing a straw man called "the Cambrian explosion hypothesis," defined as a claim "that the phyla and even classes of the animal kingdom originated in a rapid evolutionary radiation at the base of the Cambrian" (p. 12386). They then present their early splitting dates as a refutation of this conjecture: "We can use our results to

Cambrian explosion as an anatomical episode in the differentiation of *Baupläne* remains equally comfortable with either genealogical alternative. The question of one *vs.* ten 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. But unless lateral transfer can be validated at this multicellular level, or unless inventions of this magnitude can be so massively and coincidentally convergent, then the transformation of 10 tiny worms into the larger and well differentiated *Baupläne* of Cambrian phyla suggests an external trigger—the hypothesis traditionally favored by paleontologists in any case. (The venerable oxygen hypothesis maintains pride of ancestry, but the recent claim for melting of a "snowball earth" sometime before the Cambrian transition may well represent an even more plausible environmental trigger—see Hoffman et al., 1998; Hyde et al., 2000.)

In any case, and *pace* Bromham et al., the argument for the reality of the Cambrian explosion as an anatomical event does not depend upon the purely negative evidence of unfound fossil complexity in earlier strata, but includes several strongly positive paleontological assertions. In Darwin's time, and for nearly 100 years thereafter until the 1950's, the Precambrian fossil record stood entirely and embarrassingly blank. But paleontologists have not kept their subsequent discoveries hidden as a trade secret, and the richness of our current Precambrian record, particularly for the 100 million years preceding the Cambrian explosion, has been widely reported (Conway Morris, 1998; Gould, 1989c; McMenamin and McMenamin, 1990, for just a few among several entire books, written for general audiences on the subject). Thus, the absence of complex bilaterians before the Cambrian explosion rests upon extensive examination of appropriate sediments replete with other kinds of fossils, and located on all continents.

For example, the earth's first prominent assemblage of animals, named the Ediacara fauna for the Australian locality of its first discovery but now known from all continents, lived from about 600 million years ago right up to the explosion, with perhaps a few forms surviving beyond. These large creatures (up to a meter in length in one case, though most specimens occupy the range of centimeters to decimeters) tend to be highly flattened in form, composed of numerous sections that seem to be "quilted" together (certainly not segmented in any metameric way), and appear to possess no body openings. Although some researchers have sought the origin of a few bilaterian phyla within this fauna (Fedonkin and Waggoner, 1997), the comparisons seem farfetched and many paleontologists regard the Ediacaran animals as an early expression of pre-bilaterian possibilities of diploblast design (with modern cindarians and a few other groups surviving as a remnant of this fuller diversity), while other experts have regarded them as an entirely separate (and failed) experiment in multicellular life (Seilacher, 1989) or even as a group of marine lichen (Retallak, 1993)!

In any case, these Ediacaran fossils are soft bodied, and their preservation

confidently reject the Cambrian explosion hypothesis, which rests on a literal interpretation of the fossil record" (p. 12388). Of this paleontological record, they conclude (p. 12388): "It seems probable that metazoan diversity is recorded for the first time in the Cambrian because of a combination of ideal fossilization conditions and the advent of hard parts, or larger bodies, or both, that make many animal lineages 'visible' in the fossil record."

But I don't know a single paleontologist who would ever have formulated such a "Cambrian explosion hypothesis"—if only because the claim makes no logical sense, and can be confuted, in any case, by well-known paleontological data. Paleontologists have never regarded the Cambrian explosion as a genealogical event—that is, as the actual time of initial splitting for bilaterian phyla from a single common ancestor that, so to speak, crawled across the Precambrian-Cambrian boundary all by its lonesome. 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. The facts of the Cambrian explosion remain quite agnostic with respect to the two views about branching times now contending in the literature—Ayala *et al.*'s (1998) claim for divisions quite near the anatomical explosion, and Wray *et al.*'s (1996) and Bromham *et al.*'s (1998) argument for earlier splittings more than a billion years ago. After all, genealogical splitting and anatomical divergence of basic design represent quite different (albeit related) phenomena with no necessarily strict correlation, as exemplified in the following analogy:

If a group of Martian paleontologists had visited the earth during the Eocene epoch, they would have encountered two coexisting, and scarcely distinguishable, species of the genus *Hyracotherium*. If they had then followed the subsequent history of the lineages, they would have watched one species differentiate into the clade of rhinoceroses and the other into the clade of horses. But if a modern commentator then concluded that horses and rhinos had existed as distinct designs in their modern form (lithe runners *vs.* horned behemoths) since the Eocene, we would laugh at such a silly confusion, and point out that splitting times cannot be equated with completed anatomical divergence—especially under conventional views of Darwinian gradualism! After all, the Eocene visitors had only observed two effectively identical cousins, and could not have known that each would serve as progenitor for a highly distinct clade.

Similarly, the facts of the Cambrian explosion cannot distinguish whether —to continue with my earlier image—one tiny worm, or ten tiny worms, crawled across the Cambrian boundary as bilaterian precursors. The Cambrian explosion, as an anatomical argument, merely holds that if ten Precambrian worms formed the pool of Cambrian ancestors, they probably looked as alike as those two *Hyracotherium* species that engendered horses and rhinos.

I do not claim that the issue of one *vs.* ten tiny worms holds no relevance for other aspects of evolutionary theory, but only that the factuality of the

on all continents surely suggests that any coeval bilaterians with hard parts (or even with soft anatomy to match the Ediacarans) should be easily collectable. We do, in fact, have strong evidence for bilaterian presence in late Precambrian times, but not in a form that would lead us to postulate the anatomical complexity and specificity that first appears in the Cambrian explosion itself. Xiao et al. (1998) reported the discovery of embryos representing the blastomeres of the first few cleavage stages of apparent bilaterians (from rocks about 570 million years old, in early Ediacaran times), and from strata with a style of phosphatic replacement that can only preserve such tiny organisms. (See Chen et al., 2000, for expansion and corroboration of this interpretation.)

More importantly, paleontologists have documented a fairly rich record of benthic tracks and trails (but no body fossils) that could not have been made by the sessile or planktonic Ediacaran organisms and have, by consensus of all experts, been regarded as bilaterian in origin. But—and here's the rub— these trackways are very small, measuring 5 mm in diameter at a maximum, with most only 1 mm or so in width (see Valentine and Collins, 2000). Moreover, these tracks and trails do not extend deeply into Precambrian time. Hughes (2000, p. 64) states: "Traces made by bilaterians extend back to about 550 million years at least, but earlier sediments are famous for their undisturbed sedimentary lamination. The rise of animals able to mine organic resources in sediments in complex ways officially defines the base of the Cambrian."

Thus, positive evidence indicates only a late Precambrian origin for bilaterians of any kind. The same data imply that all Precambrian bilaterians ranged in size from the microscopic to the barely visible, and that the Cambrian boundary marks a real and geologically sudden appearance of both large complex bilaterian body fossils, and a major change in the size and complexity of their tracks and trails (Knoll and Carroll, 1999). We must then ask whether, in our highly non-fractal and allometric world, the anatomical complexity underlying and potentiating the scope of the Cambrian explosion could have originated in such tiny animals. (The fact that substantial complexity can be retained in some miniaturized offshoots of large bilaterians does not permit the reverse inference of initial invention at such small sizes.)

Most experts have argued that the complexity and diversity of bilaterian anatomy, as achieved in the Cambrian explosion, could not have evolved in creatures limited to a few mm at most in their major body axis. (Moreover, the simplicity of Precambrian tracks and trails also suggests limited styles of motion and feeding strategies in the tiny creatures that made the trace fossils.) The most popular and interesting conjecture for a biological trigger to a non-artifactual Cambrian explosion (Davidson et al., 1995; Peterson et al., 1997; Peterson and Davidson, 2000) calls upon markedly increased body size potentiated by the evolution of set-aside cells—a mechanism that permitted the tiny and anatomically simple ancestral bilaterians to circumvent ancient constraints of size and to enter a domain of magnitude where modern anatomical

complexity could evolve. (But see Valentine and Collins, 2000, who challenge Davidson et al.'s key assumption that the tiny larvae of indirectly-developing modern bilaterians represent plesiomorphic models for ancestral adults before the evolution of set-aside cells.)

Thus, given that the Cambrian explosion was a real event, and that the basic homologies and developmental rules of bilaterian design (particularly as manifested in the spatial and temporal colinearity of hoxology) had already been established in the ancestors of the explosion (those one to ten tiny worms, if you will), then we may infer that bilaterian diversity unfolded along the channels of developmental patterns held in common from the beginning of this holophyletic clade. Bilaterian diversity, in other words, represents an extensive set of modifications and tinkerings upon a basic pattern set by history at the outset, and then adumbrated in one geologically brief episode to establish all fundamental building plans. Forever after, for more than half a billion years, the subsequent evolution of complex animals—that is, all bilaterian history since the Cambrian explosion—has been restricted to much more limited permutation within the confines of these early, congealed designs (however glorious and richly varied the range of ecological results).

Once we accept these premises, one broad question, rather more philosophical in nature and famously contentious given the assumptions of our cultural histories and our anthropophilic propensities, must be aired (see Gould, 1989c, and Conway Morris, 1998, for the alternative positions, and also our explicit debate in Conway Morris and Gould, 1998): If the basic developmental patterns of bilaterians arose quickly, and have remained fixed in basic form since then, do these historical invariants represent a set of mechanically limited and excellent, perhaps even optimal, designs that natural selection would have established in much the same way at any time and under any ecological or geological regime? Or do they represent just one possible solution among numerous entirely plausible alternatives of strikingly different form, each yielding a subsequent history of life entirely different from the outcome actually experienced on earth? In the second alternative, life's history unfolds with much of the unpredictability and contingency so famously displayed, for example, in the history of human cultural diversity—and the accident of a common developmental starting point for subsequent bilaterian diversity then assumes even more importance as a golden happenstance directly responsible for the particulars of the world we know.

Historical constraint based on developmental homology assumes great importance in either case, but if the particular constraints that actually set the channels of bilaterian diversity could only have arisen within a narrow range of basically similar and workable states, then much of life's pageant unfolds by predictable regularities of natural selection. If, however, the developmental plans actually established in the Cambrian explosion—albeit eminently workable, and therefore exploited by natural selection to build the particulars of life's later successes and failures—represent only one contingently-achieved set among a broad realm of alternatives (each "equally pleasing" to

natural selection), then life's actual pageant on earth becomes highly unpredictable, and the happenstance of a realized beginning (the historical constraints of bilaterian developmental homology) assumes a far more prominent role in shaping the subsequent history of life.

My own arguments for contingency have been well aired (Gould, 1989c; see subsequent debate on the key technical issue in Gould, 1991a; Briggs et al., 1992, with response by Foote and Gould, 1992), and this debate only addresses the role of historical constraints in setting the actual pathways of life's singular history on earth, and not the existence of the constraints themselves (the subject of this section). Thus, I will not discuss the important question of predictability vs. contingency much further, except to clarify the problem by noting that questions of contingency enter our understanding of evolutionary pattern at two levels of inquiry about the Cambrian explosion and its consequences.

First, we must ask if the basic bilaterian homologies themselves, particularly the *Hox* rules, represent an optimal solution that natural selection would have constructed in any case, or a workable happenstance among many alternatives. The very fact that some homonomous bilaterian phyla possess a complete complement of *Hox* genes, and that the original function of these genes therefore cannot match their present role in controlling the various downstream cascades that specialize and differentiate the sequence of structures along the AP axis, speaks strongly for contingency—because current utilities must therefore represent cooptations from different original functions, rather than primary adaptations. Such cooptation, expressing the principle of "quirky functional shift" (see Chapter 11, pp. 1218–1229 for full discussion), inevitably suggests (but admittedly does not prove) a high degree of fortuity, as implied by the required capacity of features built for one function to act in another way that could not have influenced or regulated their original construction by any functional evolutionary mechanism like natural selection.

In this particular case, for example, Deutsch and Le Guyader (1998) have suggested a historically prior function for *Hox* (and other zootype) genes in designing "an appropriate neuronal network in bilaterian animals" (p. 713). Recognizing the relevance of this idea to the issue of contingency and the Cambrian explosion (1998, p. 716), they write: "Hence, the presence, before the Cambrian explosion, of a large number of *Hox* genes, whose domains of activity extend from the post-oral head to the abdomen, cannot be accounted for by a function in driving morphological diversity. Another role has to be assumed for the ancestral function of the *Hox* genes. We postulate that the zootype genes primitively specified neural identity."

Second, we must ask if the realized variants that congealed so quickly as specialized and differentiated body plans (the major bilaterian *Baupläne*)—permitting no further origin of novel anatomies sufficiently distinct to warrant taxonomic recognition as phyla—represent a predictable set of "best solutions" within the broad possibilities of historical constraint permitted by shared developmental rules? Or do they constitute a subset of workable, but

basically fortuitous, survivals among a much larger set that could have func-
tioned just as well, but either never arose, or lost their opportunities, by his-
torical happenstance? I admit my partisanship for the latter position (Gould,
1989c) and freely acknowledge that my judgments have won some support,
but no consensus to say the least (Conway Morris, 1998). I would only point
out that even the strongest opponents of contingency admit that arthropod
disparity (the measured range of anatomical designs, not the number of spe-
cies) had reached a fully modern range in the Burgess Shale faunas (Middle
Cambrian, about 10 million years after the explosion)—and that more than
500 million years of additional arthropod evolution has not expanded the
scope of anatomical disparity at all (Briggs et al., 1992; Foote and Gould,
1992, present evidence for the counter view that Cambrian disparity ex-
ceeded modern levels, despite much lower species diversity). I would also
urge my colleagues to spend more time studying Cambrian "oddballs" that
do not easily fit into recognized higher taxa, including *Xidazoon* among "or-
phan" taxa (Shu et al., 1999), or *Fuxianhuia* among arthropods that do not
belong to any recognized class (Chen et al., 1995), and not to focus so
strongly, as most studies have done in recent years, upon cladistic attempts to
place all Cambrian forms at least into the stem regions of major phyla, if
shared derived markers of crown groupings bar their entry—a strategy that
leads researchers to ignore the autapomorphies of these peculiar taxa, and to
coax other features into plesiomorphy with modern taxa.

CHANNELING THE SUBSEQUENT DIRECTIONS OF BILATERIAN HISTORY
FROM THE INSIDE. If the bilaterian ancestor possessed a full complement of
Hox genes, and if all major variants upon this initial system had already con-
gealed by the end of the Cambrian explosion, then subsequent bilaterian evo-
lution must unfold within the secondary strictures of these realized specializa-
tions upon an underlying plan already channeled by primary constraints of
the common ancestral pattern. But lest we begin to suspect that rigid limita-
tion must represent the major evolutionary implication of such constraint,
I must reemphasize the positive aspect of constraint as fruitful channeling
along lines of favorable variation that can accelerate or enhance the work of
natural selection. Moreover, the evolutionary flexibility of developmental
channels achieves its most impressive range—as Chapter 11 will discuss as its
primary subject—through the crucial principle of cooptation, or the extensive
and inherent capacity of genes evolved for one particular function to operate,
through evolutionary redeployment, in strikingly different adaptive ways.

Among "higher" triploblast phyla of markedly divergent design, echino-
derms represent the obvious test case for studying the flexibility of homolo-
gous developmental genes. With their remarkable autapomorphies of radial
symmetry, calcitic endoskeleton, and a water vascular system for circulation,
how could these creatures evolve within the confines of a genetic regulatory
system that builds bilaterial, axially specialized organisms with blood vascu-
lar systems in both their immediate sister phylum (the vertebrates) and in
plesiomorphic taxa of more distant common ancestry (the protostome phyla