such observations are less an indictment of extrapolation than a demonstration that the greatest uncertainties affecting future mortality trends derive from social and political, rather than technological, factors.

Although imperfect, the appeal of extrapolation lies in the long-term stability of the historical mortality decline, which can be attributed to the complex character of the underlying process. This combination of stability and complexity should discourage us from believing that singular interventions or barriers will substantially alter the course of mortality decline in the future. In this situation, the burden of proof lies with those who predict sharp deviations from past trends. Such predictions should be based on theoretical results that are firmly established and widely accepted by the scientific community. Certainly, history can be overruled by a genuine consensus within the scientific community, but not by unproven theories, intuition, or speculation.

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11. A French demographer asserted in 1978 that the biological limit to human life expectancy at birth was 73.8 years for men and 80.3 years for women. Life expectancy in Japan exceeded these values in 1982 for men and in 1985 for women. See J. Bourgeois-Pichat, *Popul. Bull. United Nations* **11**, 12 (1978); see also the Berkeley Mortality Database (http://demog.berkeley.edu/wilmoth/mortality). Similarly, the United Nations predicted in 1973 that life expectancy at birth for developed countries would equal 72.6 years in 1985–90, though later estimates showed that the life expectancy actually attained was 74.0 years. Corresponding figures are 58.7 and 60.5 years for developing countries, and 60.7 and 63.0 years for the world. See United Nations, *World Population Prospects as Assessed in 1973* (United Nations, New York, 1977); *World Population Prospects: The 1994 Revision* (United Nations, New York, 1995).
12. Data from the Social Security Administration, 1997. Death rates are standardized to the U.S. population in mid-1990. The break in trends occurs ~1954 for life expectancy and 1940 for death rates.
13. I thank R. Lee, S. Horiuchi, K. Wachter, and J. Campisi for helpful comments.

EVOLUTION

One or Three Cambrian Radiations?

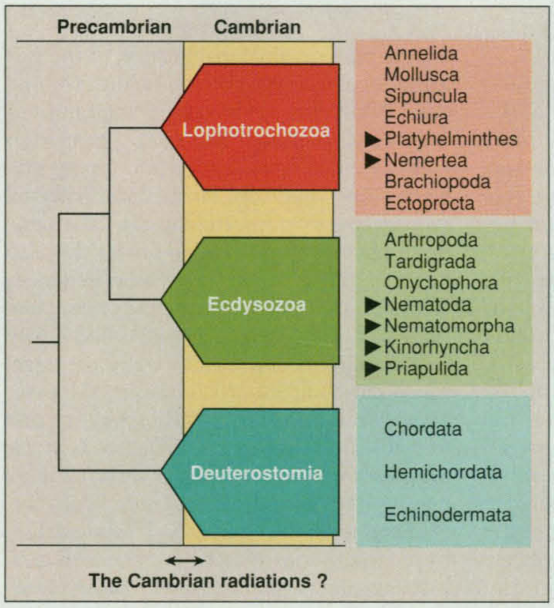
Guillaume Balavoine and André Adoutte

The evolutionary phenomenon known as the "Cambrian explosion" was the sudden appearance of a modern-looking Burgess shale-like fauna with bilateral symmetry, early in the Cambrian period. This major event has increasingly attracted the interest of paleontologists and, more recently, of molecular phylogeneticists. Now, Aguinaldo *et al.* (*1*) have provided some striking new data that may allow a reinterpretation of animal phylogeny and may have a profound bearing on understanding of the Cambrian explosion.

The Cambrian bilaterians appeared shortly after the extinction of the Vendian Ediacara fauna. Vendian organisms have been described as triploblasts, diploblasts, or even multicellular organisms unrelated to metazoans (*2*). However, the few existing interpretations of some of these elusive organisms as direct relatives of the Cambrian triploblasts remain ambiguous (*3*), although trace fossils (*4*) and Precambrian embryos (*5*) suggest that triploblasts were likely to be present. What did the ancestors of the bilaterians look like, and why do they not appear more conspicuously in the Precambrian fossil record?

In traditional, morphologically based phylogenies, animals are divided into two-layered radially symmetrical animals and three-layered bilaterally symmetrical ones (or Bilateria). These Bilateria are further subdivided according to their internal organization: the Acoelomata, lacking a body cavity (mainly the platyhelminths and nemertines); the Pseudocoelomata (nematodes and some other minor phyla), which have a "primitive" internal cavity outside the mesoderm, presumably derived from the embryonic blastocoele; and the Coelomata, which have true coelomic cavities splitting the mesoderm. According to the traditional intellectual bias for increasing complexity in evolution, the acoelomates were seen as emerging at the base of the bilaterian family tree, followed by the pseudocoelomates and finally the coelomates, whose coelome allowed more complex body plans and larger sizes to evolve. These coelomates are further divided into protostome coelomates and deuterostomes, essentially according to the ontogenic origin of the mouth.

A new vision of the phylogenetic relationships between metazoan phyla has taken shape in the past 2 years through the investigations of the evolution of the 18S ribosomal DNA. Sequences are now available for almost all of the phyla, and a handful of recent reports, in good agreement with each other, now strikingly challenge the traditional views. In a consensual 18S ribosomal DNA tree, the Bilateria are divided in two large branches, the Deuterostomia and the Protostomia. The Protostomia are further divided in two new (and puzzling for many



Watching an explosion. Divisions of the bilaterian family tree, showing three lineages of coelomates, among which the acoelomates and pseudocoelomates are scattered (arrows).

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zoologists) groups, the Lophotrochozoa (*6*) (combining Eutrochozoa and Lophophorata) and the Ecdysozoa (*1*) (moulting animals). The basal status of the acoelomates and the pseudocoelomates is vanishing in view of this new evidence: Most of the acoelomates do not show an early emerging position but are found in the Lophotrochozoa together with coelomate phyla (*1, 7–9*). The pseudocoelomates, or aschelminths, do not form a monophyletic group: Rotifers and gastrotriches are grouped with the lophotrochozoans (*8*), whereas kinorhynchs, priapulids, nematodes, and nematomorphs are found with the arthropods in the Ecdysozoa (*1, 8*). The traditional phylogeny is thus turned upside down. The bilaterian tree is divided in three great coelomate lineages (see figure), among which the simply organized acoelomates and pseudocoelomates are scattered. It is quite comforting that data of a completely different type, namely, the evolution of the *Hox* gene cluster, appear to confirm some aspects of the above phylogeny, such as the affinities of flatworms (*9*).

Another remarkable feature of these trees is the consistently poor resolution of the relationships within these three superphyla, as illustrated by the failure to retrieve the monophyly of well-recognized phyla such as annelids, molluscs, and arthropods (*1, 10*). This absence of resolution may positively indicate a rapid process of radiation that occurred at the beginning of the history of each of these branches (*11*). This corresponds well with the paleontological data, as the earliest unambiguous fossil representatives of the superphyla all appear suddenly in the Lower Cambrian [mollusks and brachiopods (*12*) as lophotrochozoans, arthropods and priapulids as ecdysozoans, echinoderms (*13*) and chordates (*14*) as deuterostomes].

This remarkable trifurcation of the Bilateria leads us to a new interpretation of the Cambrian explosion as simultaneous radiations of three long-separated stem lineages. The lineages diverged well back in the Precambrian but were poorly diversified before the Cambrian. Attempts to date the protostome-deuterostome divergence with several types of molecules have given conflicting dates of either more than one billion years (*15*) or just 670 million years (*16*). These calculations nevertheless agree on the existence of a large fossil gap between the separation of the three stem branches and their actual appearance in the fossil record. It has been suggested that this gap may be due to the fact that the Vendian ancestors of the large coelomates were tiny animals, unlikely to give fossils (*17*). This hypothesis supposes that a major event allowed the size of metazoans to increase dramatically at the beginning of the Cambrian. However, large-sized metazoans were already present during the Vendian. We think that the three-branched bilaterian phylogeny also strongly contradicts this view. If these tiny ancestral worms had existed before the Cambrian, their hypothetical, unchanged, simply organized descendants (platyhelminths, nematodes, gastrotriches, rotifers, and so forth) would root back to a "basal" position in the bilaterian tree, forming a "phylogenetic lawn" in which the three coelomate branches would be rooted. Instead, acoelomates and pseudocoelomates are found dispersed among the coelomate phyla in the two protostomian branches. Thus, they are likely to be derived, secondarily simplified forms. We suggest that the ancestors of the three coelomate branches may have been macroscopic coelomate animals. In that case, these macroscopic animals being rare or restricted to environments unlikely to allow fossilization may explain their absence in the Precambrian fossil record. However, their already complex body plans would have constituted the necessary preadaptations for their explosive diversification in the Cambrian.

Should this hypothesis of three simultaneous radiative events be accepted, it would also argue in favor of an external cause for the Cambrian explosion. One cannot resort to a single internal genetic mechanism (such as the "invention" of the *Hox* cluster) to explain the radiation of three long-separated lineages. An ecological type of explanation [such as the rapid building up of new complex trophic networks in the context of an ecological vacuum (*18*)] should thus be investigated.

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CHEMISTRY

Rethinking Solution NMR

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In the 50 years since publication of the first solution nuclear magnetic resonance (NMR) data, NMR has evolved from explorations of esoteric quantum mechanical properties (nuclear angular momenta and dipole moments) into what is by far the most powerful form of spectroscopy employed by the practicing chemist. Part of the reason for this evolution is the maturation of radio frequency technology: Staggeringly complex manipulations with radio frequency pulses and pulsed field gradients are trivial to implement. Much more importantly, however, the theoretical framework of NMR is mature and tractable. Researchers can calculate how the magnetization evolves under such complex manipulations and can optimize pulse sequences to extract structural information. Even undergraduate students can readily analyze one- and two-dimensional solution spectra of moderately sized molecules (with, for example, 100 hydrogen atoms), and complete analyses of the spectra of proteins with molecular masses of order 25 kD have become commonplace. Nonetheless, one of the most intriguing modern research directions in NMR is the rethinking of the assumptions behind its "standard picture." This rethinking, as reported for example by Glaser *et al.* (*1*) on page 421 of this issue, is leading toward substantially improved pulse sequences, permitting measurements of entirely new parameters, and extending the range of sample sizes and molecular sizes accessible by NMR.

One might argue that NMR spectra should be exceedingly difficult to interpret. Imagine that we could detect the signal from a single

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