

**Table 1. Associations between transmission mode (STD: sexually transmitted disease; OI: other infectious disease) and some characteristics of disease ecology<sup>a</sup>**

Disease characteristic	Prediction	Statistical support		
		Means analysis	PCA <sup>b</sup>	Path analysis <sup>c</sup>
Mortality/severity	OID>STD	Yes	Yes	Yes
Length of infection	STD>OID	Yes	Yes	Yes
Localization of infection	OID>STD	Yes	Yes	Yes
Host immunity	OID>STD	Yes	Yes	Yes (indirect)
Host range	OID>STD	Yes	Yes	Yes
Sterility	STD>OID	No	Yes	Yes?

<sup>a</sup>Adapted from Ref. 2.

<sup>b</sup>PCA, Principal Components Analysis.

<sup>c</sup>Results presented for path analysis refer to a model postulating a causal effect of transmission mode.

some time worked on a system which provides support for these ideas. Another smut diseases of flowering plants are transmitted by pollinators and are therefore plant STDs; although the presence of pollinators as vectors adds some complexity, they have recently attracted attention as a model system for the study of epidemiology and ecology<sup>12</sup>. In an analysis of plant hosts of these diseases<sup>13</sup>, it was found that host species that undergo more outcrossing and had larger floral displays (both likely correlates of the extent of multiple mating) harboured more smut diseases.

Lockhart *et al.*'s work is important for several reasons. It demonstrates beyond any doubt the ubiquity of STDs, and suggests that any biologist interested in mating behaviour and parasite-mediated selection should consider the role that STDs have played in structuring the system that they work with. Second, their

analyses provide striking support for the idea that the characteristics of diseases are inextricably linked with their ecology. Finally, their work should serve as an example of the scope possible for comparative analyses of disease; even in the face of data of varying quality, collected for reasons quite unconnected with the purpose of the analysis, it is possible to uncover unsuspected patterns.

#### Acknowledgements

We are grateful to A. Buckling, M. Mackinnon and P. Thrall for comments, and to NERC and BBSRC, respectively, for research fellowships.

**Ben C. Sheldon**  
**Andrew F. Read**

*Institute of Cell, Animal & Population Biology,  
University of Edinburgh, West Mains Road,  
Edinburgh, UK EH9 3JT*

#### References

- Smith, G. and Dobson, A.P. (1992) Sexually transmitted diseases in animals, *Parasitol. Today* 8, 159–166
- Lockhart, A.B., Thrall, P.H. and Antonovics, J. (1996) Sexually transmitted diseases in animals: ecological and evolutionary implications, *Biol. Rev.* 71, 415–471
- Getz, W.M. and Pickering, J. (1983) Epidemic models: thresholds and population regulation, *Am. Nat.* 121, 892–898
- Anderson, R.M. and May, R.M. (1991) *Infectious Diseases of Humans: Dynamics and Control*, Oxford University Press
- Ewald, P.W. (1994) *Evolution of Infectious Disease*, Oxford University Press
- Bull, J.J. (1994) Virulence, *Evolution* 48, 1423–1437
- Read, A.F. (1994) Evolution of virulence, *Trends Microbiol.* 2, 73–76
- Frank, S.A. (1996) Models of parasite virulence, *Q. Rev. Biol.* 71, 37–78
- Freeland, W.J. (1976) Pathogens and the evolution of primate sociality, *Biotropica* 8, 12–24
- Hamilton, W.D. (1990) Mate choice near or far, *Am. Zool.* 30, 341–352
- Sheldon, B.C. (1993) Sexually transmitted disease in birds: occurrence and evolutionary significance, *Philos. Trans. R. Soc. London Ser. B* 339, 491–497
- Klatz, O. and Schmid, B. (1995) Plant venereal disease: a model for integrating genetics, ecology and epidemiology, *Trends Ecol. Evol.* 10, 221–222
- Thrall, P.H., Biere, A. and Antonovics, J. (1993) Plant life-history and disease susceptibility: the occurrence of *Ustilago violacea* on different species within the Caryophyllaceae, *J. Ecol.* 81, 489–498

## The breath of life – did increased oxygen levels trigger the Cambrian Explosion?

A literal reading of the fossil record would suggest that something uniquely strange went on during the first 10 million years of metazoan evolution. Metazoan animal life as we know it did not appear until the Cambrian, 544 million years ago<sup>1,2</sup> (apart from the enigmatic 560–590 million year old Ediacaran fauna). But just 10 million years later the metazoans had achieved their maximum Cambrian diversity: well-preserved fossil representatives of two thirds of all known phyla are present in rocks about 533 million years old. A flurry of recent research agrees with Darwin's suggestion<sup>3</sup> that the absence of fossil evidence of the metazoans before the Cambrian Explosion is not evidence

that the metazoans were absent. The Cambrian Explosion may not record the origin and explosive radiation of metazoan phyla, but instead it may record an extraordinary period when most of the known phyla simultaneously acquired both the large size and hard skeletons required for fossilization. Several recent independent studies provide molecular clocks that date the origin of the metazoans to at least 400 million years before the Cambrian. Developmental arguments suggest that there may have been a long period of cryptic evolution when metazoans resembled modern planktonic larvae (which do not fossilize). Finally, recent analysis of the ancient atmosphere<sup>4</sup> may have provided a reason

why so many phyla first appear in the fossil record simultaneously. The Cambrian Explosion may have been triggered when rising oxygen (O<sub>2</sub>) concentrations passed a threshold that permitted the development of large size and hard skeletal structures.

The origin of the metazoans has been put firmly back into the middle of the proterozoic era, at about 1000 million years ago, by two independent molecular clock estimates of the times of divergence of the major animal groups. Doolittle and co-workers<sup>5</sup> use amino acid sequences from 57 different proteins, and Wray and co-workers<sup>6</sup> use DNA sequences from seven genes to provide molecular clocks calibrated against the vertebrate fossil record (reviewed in the previous issue of *TREE* by Michael Bell<sup>7</sup>). The amino acid clock suggests a divergence time for the two main metazoan groups (Deuterostomes and Protostomes) of about 675 million years ago, while the DNA sequence clock suggests that this split had already occurred

about 1200 million years ago. Both sets of data point to an origin of the metazoans at about the middle of the proterozoic at least 500 million years before the Cambrian Explosion.

But if metazoans were around for almost 500 million years before the Cambrian Explosion why did they leave no fossil remains? Only about two thirds of the extant phyla have left any fossil record, and the missing phyla (e.g. nematodes) tend to be small, soft-bodied, planktonic or interstitial animals. Davidson *et al.*<sup>8</sup> suggest from developmental evidence that the metazoans underwent a long period of 'cryptic' evolution when the seas teemed with planktonic metazoans much like modern planktonic larvae. Circumstantial palaeontological evidence supports this possibility. Trace fossils and even possible fossilized metazoan faecal pellets are widespread from about 1000 million years ago onwards, and the diversity and abundance of stromatolites declined markedly at this time – possibly as a result of metazoan grazing and burrowing activity. It seems likely that the metazoans originated around 1000 million years ago, and the Cambrian Explosion records a period when species distributed across a wide range of phyla suddenly and simultaneously became large enough to leave soft-body fossils, and developed the hard shell-like skeletons that make the normal fossilization process possible. However, that still leaves the puzzle of why metazoan animals spread across the whole range of phyla should suddenly develop the ability to fossilize at the same time.

One possible explanation of the sudden simultaneous evolution of large size and of hard skeletons is that both these features demand a high environmental O<sub>2</sub> concentration. Atmospheric O<sub>2</sub> is a by-product of photosynthesis, and O<sub>2</sub> concentrations are known to have risen during the proterozoic. Large (macroscopic) size means that the distance from the external environment to internal metabolically active tissues is large. A high environmental O<sub>2</sub> concentration is required to drive the diffusion of O<sub>2</sub> any distance into the body tissues. Large size in metazoans is associated with a high metabolic rate and this also requires a high O<sub>2</sub> concentration. Metazoan animals may also require a high environmental O<sub>2</sub> concentration because the synthesis of the ubiquitous structural protein collagen requires a relatively high O<sub>2</sub> concentration, and this fact may well underlie the sudden simultaneous acquisition of hard parts by a wide range of phyla at the start of the Cambrian. Indeed, hard parts themselves may have only become feasible once O<sub>2</sub> concentrations passed some threshold level – a hard shell or exoskeleton will inevitably reduce the

exposed surface available for the exchange of respiratory gases.

Recently, Canfield and Teske<sup>1</sup> have presented evidence that around 1000 million years ago atmospheric O<sub>2</sub> levels passed a threshold concentration that triggered a widespread radiation of sulphide-oxidizing bacteria. They suggest that the radiation of eukaryotes, and within them the metazoans, may also have been driven by rising atmospheric O<sub>2</sub> concentrations.

Pure cultures of sulphate-reducing bacteria produce sulphide deposits that are enriched in the <sup>34</sup>S isotope by 1.8±1%. However, marine sulphide deposits are typically enriched in the <sup>34</sup>S isotope by 5.1±1%. Sulphide-reducing bacteria make their living by reducing sulphate to sulphide, but in areas with steep opposing concentration gradients of O<sub>2</sub> and sulphide, there also exist sulphide-oxidizing bacteria that make their living by oxidizing sulphide back to sulphur or sulphate. Canfield and Teske<sup>1</sup> argue that the enhancement of the <sup>34</sup>S isotope in recent marine sulphide deposits is due to the repeated fractionation as sulphate is bacterially reduced to sulphide and then oxidized back to sulphate by sulphide-oxidizing bacteria in a continuous oxidative sulphur-cycle. They suggest that a distinct change in the sulphur isotope ratios in marine sulphide deposits from between 640 and 1050 million years ago indicates the time when atmospheric O<sub>2</sub> concentrations first became high enough to permit the oxidative sulphur-cycle to operate and sulphide-oxidizing bacteria to evolve.

Sulphide-oxidizing bacteria require steep opposing sulphide and O<sub>2</sub> concentration gradients for their metabolic activity. Some minimum level of atmospheric O<sub>2</sub> concentration must have been present in the atmosphere before sulphide-oxidizing bacteria could have evolved. Canfield and Teske argue that once atmospheric O<sub>2</sub> concentrations reached 5% of present levels marine coastal sediments less than 200 m deep would have provided favourable conditions for the evolution of sulphide-oxidizing bacteria, and at an atmospheric O<sub>2</sub> concentration of 18% of current levels half of all coastal marine sediments would have been a suitable habitat for sulphide-oxidizing bacteria. By using a 16S rRNA molecular clock, they are able to date the origin of the sulphide-oxidizing bacteria to an absolute maximum date of 1440 million years ago, a date which is in broad agreement with the timing of the change in the sulphur isotope ratios in marine sulphide deposits that they report.

Canfield and Teske's data suggest that atmospheric O<sub>2</sub> concentrations passed from below to above 5–18% of current levels somewhere between 640 and 1050 million years ago, and this rise in atmospheric

O<sub>2</sub> levels triggered the radiation of sulphide-oxidizing bacteria. They suggest that this rise in atmospheric O<sub>2</sub> concentrations may also have triggered the origin of the eukaryotes and the radiation of the metazoans. However, there remains an unsolved problem: the rise in the concentration of O<sub>2</sub> in the ancient atmosphere identified by Canfield and Teske coincides reasonably well with the suggested time of origin of the metazoans, but pre-dates the Cambrian Explosion by some 500 million years. Canfield and Teske have identified a possible threshold which, once crossed, permitted the evolution of the sulphur-oxidizing bacteria. Was the Cambrian Explosion triggered as the O<sub>2</sub> concentration in the ancient atmosphere passed another threshold, a threshold that permitted the development of large size and of hard skeletal structures?

Adrian L.R. Thomas

Dept of Zoology, Oxford University,  
South Parks Road, Oxford, UK OX1 3PS

## References

- 1 Conway Morris, S. (1993) The fossil record and the early evolution of the Metazoa, *Nature* 361, 219–225
- 2 Bowring, S.A. *et al.* (1993) Calibrating rates of early cambrian evolution, *Science* 261, 1293–1298
- 3 Darwin, C. (1859) in *On the Origin of Species by Means of Natural Selection*, p. 286, Murray
- 4 Canfield, D.E. and Teske, A. (1996) Late proterozoic rise in atmospheric oxygen concentration inferred from phylogenetic and sulphur-isotope studies, *Nature* 382, 127–132
- 5 Doolittle, R.F. *et al.* (1996) Determining divergence times of the major kingdoms of living organisms with a protein clock, *Science* 271, 470–477
- 6 Wray, G.A., Levinton, J.S. and Shapiro, L.H. (1996) Molecular evidence for deep Precambrian divergences among Metazoan Phyla, *Science* 274, 568–573
- 7 Bell, M.A. (1997) Origin of metazoan phyla: Cambrian explosion or proterozoic slow burn? *Trends Ecol. Evol.* 12, 1–2
- 8 Davidson, E.H., Peterson, K.J. and Cameron, R.A. (1995) Origin of bilaterian body plans: evolution of developmental regulatory mechanisms, *Science* 270, 1319–1325

## Students!

50% discount on *Trends in Ecology & Evolution* subscriptions!

For details see subscription card bound in this issue