some time worked on a system which pro-
vides support for these ideas. Anther-smut
diseases of flowering plants are trans-
mitted by pollinators and are therefore
plant STDs; although the presence of pol-
linators as vectors adds some complexity,
they have recently attracted attention as
a model system for the study of epidemi-
ology and ecology. In an analysis of plant
hosts of these diseases, it was found that
host species that undergo more outcross-
ning and had larger floral displays (both
likely correlates of the extent of multiple
mating) harboured more smut diseases.

Lackhart et al.’s work is important for
several reasons. It demonstrates be-
Yond 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 sys-
tem 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
element of the scope possible for com-
parative 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.

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Ben C. Sheldon
Andrew F. Read

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

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

A

lteral reading of the fossil record
would suggest that something uniquely
strange went on during the first 10 million
years of metazoan evolution. Metazoan an-
imal life as we know it did not appear un-
til the Cambrian, 544 million years ago1–2
(apart from the enigmatic 560–590 mil-

lion year old Ediacaran fauna). But just 10
million years later the metazoans had
achieved their maximum Cambrian diver-
sity: well-preserved fossil representatives
of two thirds of all known phyla are pres-
ent in rocks about 533 million years old.
A flurry of recent research agrees with
Darwin’s suggestion3 that the absence of
fossil evidence of the metazoans before
the Cambrian Explosion is not evidence
that the metazoans were absent. The Cam-
brian 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 sim-
ultaneously acquired both the large size
and hard skeletons required for fossiliza-
tion. Several recent independent studies
provide molecular clocks that date the
origin of the metazoans to at least 400 mil-

lion years before the Cambrian. Develop-
mental arguments suggest that there may
have been a long period of cryptic evolu-
tion when metazoans resembled modern
planktonic larvae (which do not fossilize).
Finally, recent analysis of the ancient at-
mosphere4 may have provided a reason
why so many phyla first appear in the fos-
sil record simultaneously. The Cambrian
Explosion may have been triggered when
rising oxygen (O₂) 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 pro-
terozoic 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-
workers5 use amino acid sequences from
57 different proteins, and Wray and co-
workers6 use DNA sequences from seven
genes to provide molecular clocks cali-
ibrated against the vertebrate fossil record
(reviewed in the previous issue of TREE
by Michael Bell). 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 sug-
gests that this split had already occurred

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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. 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 metazoans 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 O₂ concentration. Atmospheric O₂ is a by-product of photosynthesis, and O₂ 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 O₂ concentration is required to drive the diffusion of O₂ any distance into the body tissues. Large size in metazoans is associated with a high metabolic rate and this also requires a high O₂ concentration. Metazoan animals may also require a high environmental O₂ concentration because the synthesis of the ubiquitous structural protein collagen requires a relatively high O₂ 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 O₂ 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 have presented evidence that around 1000 million years ago atmospheric O₂ 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 O₂ concentrations.

Pure cultures of sulphate-reducing bacteria produce sulphide deposits that are enriched in the 34S isotope by 1.8±1.1%. However, marine sulphide deposits are typically enriched in the 34S 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 O₂ and sulphide, there also exist sulphide-oxidizing bacteria that make their living by oxidizing sulphide back to sulphur or sulphate. Canfield and Teske argue that the enhancement of the 34S 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 O₂ 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 O₂ concentration gradients for their metabolic activity. Some minimum level of atmospheric O₂ concentration must have been present in the atmosphere before sulphide-oxidizing bacteria could have evolved. Canfield and Teske argue that once atmospheric O₂ 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. 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 O₂ concentrations passed from below to above 5–15% of current levels somewhere between 640 and 1050 million years ago, and this rise in atmospheric O₂ levels triggered the radiation of sulphide-oxidizing bacteria. They suggest that this rise in atmospheric O₂ 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 O₂ in the ancient atmosphere. Canfield and Teske discuss the possibility that the rise was a result of the increasing abundance of oxygenic phototrophs, or perhaps a result of the life cycle of a single organism such as a cyanobacterium.

Adrian L.R. Thomas
Dept of Zoology, Oxford University, South Parks Road, Oxford, UK OX1 3PS

References

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