distribution of the surrounding downwelling light. Deep-sea fishes that have instead evolved to detect bioluminescent point sources have eyes constructed accordingly, typically having a high spatial resolution provided by a retinal area of tightly packed visual cells arranged in a deep pit-like fovea. Their eyes, though, are often quite small, with pupils only as large as necessary to detect points of light at ecologically meaningful distances, which in the nutritionally impoverished deep may only be a few body lengths.

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1Department of Biology, University of Lund, Sölvegatan 35, S-22362 Lund, Sweden.

2Department of Biology, Duke University, Durham, NC 27708, USA.

3E-mail: Eric.Warrant@biol.lu.se

Correspondences

Neanderthal and Denisovan retroviruses in modern humans

Emanuele Marchi1,2,3, Alex Kanapin2,4, Matthew Byott3, Gikias Magiorkinis1,4, and Robert Belshaw3,5

In the June 5th 2012 issue of Current Biology, Agoni et al. [1] reported finding 14 endogenous retrovirus (ERV) loci in the genome sequences of Neanderthal and/or Denisovan fossils (both ~40,000 years old) that are not found in the human reference genome sequence. The authors [1] concluded that these retroviruses were infecting the germline of these archaic hominins at or subsequent to their divergence from modern humans (~400,000 years ago). However, in our search for unfixed ERVs in the modern human population, we have found most of these loci. We explain this apparent contradiction using population genetic theory and suggest that it illustrates an important phenomenon for the study of transposable elements such as ERVs.

The genomes of extinct human groups (archaic hominins), such as Neanderthals, are now available with high throughput sequencing technology, which can produce millions of short (~100 base) sequences called reads from fossil bone or teeth. An analysis of six in an analysis of 67 cancer patient genomes (Figure 1), and examination of another study of 43 such genomes [3] shows all seven to be present (Supplemental information). One is K113 (19p12b), which is well-described and has a frequency of 16% in modern humans [2]. The four reported Denisovan loci lacking coordinates are within repetitive or unassembled regions of the genome, and we can neither confirm nor refute their presence in the modern human population: e.g. two loci are in transposable elements called Alu’s, of which there are ~1,000,000 copies in the human genome (making up ~10% of the human genome sequence). When an ERV integrates into another transposable element, finding this ERV locus can be a formidable computational challenge because there are many paralogous copies of the integration site. Two additional loci were reported from the Neanderthal fossil, and we have found one of these.

It is unlikely that these ERV loci in the archaic hominins are contaminants from modern human DNA. Average coverage of the Denisovan genome was only about twofold and the contamination rate among the reads was estimated using several approaches to have been less than 1% [4]. We believe that the explanation lies in fundamental population genetics. With the exception of co-opted ERV loci such as syncytins [5], which could increase in frequency due to positive selection, we assume ERV loci become common by genetic drift, and the average time for a neutral allele to go to fixation is 4N selections (where N is the effective population size). Given estimates of long-term human generation time and population size [6], this is ~800,000 years. The population divergence of modern humans from the Denisovan/Neanderthal lineage is more
ERVs in fossil hominins also improve our understanding of both ERV and human evolution. When the ERV loci in modern humans have been reasonably well-sampled, fossil loci will help us build a robust mathematical model of ERV proliferation. Then, because ERV loci make easily detectable and irreversible genetic markers (the common mechanism called ‘recombinational deletion’ leaves a relict structure called a solo-LTR [9]), they might help us in the measurement of divergence dates and population sizes for these archaic hominins.

**Supplemental Information**

Supplemental Information including experimental procedures, one table and one figure can be found with this article online at http://dx.doi.org/10.1016/cub.2013.10.028.

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