

Figure 1 | Exoplanetary atmospheres. Flat transmission spectra of exoplanets during transit, such as those reported by Knutson et al. and Kreidberg et al., can result from a planet with an atmosphere that either contains high clouds (a) or that is hydrogen poor with a high mean molecular weight (b). In the cloudy case, photons from the planet's host star are blocked abruptly when they encounter the cloud layer on their way to an observer on Earth. In the hydrogen-poor case, the high molecular weight of the atmosphere allows it to be bound tightly by gravity and therefore be vertically compressed, with large changes in density over relatively small vertical scales providing a relatively sudden absorption of all the stellar photons. If the planet had a clear (cloud-free), low-mean-molecular-weight atmosphere $(not\,shown), at mospheric\,absorption\,features\,would\,be\,more\,prominent\,in\,the\,transmission\,spectrum.$

methane, carbon monoxide or carbon dioxide would have been detectable if such an atmosphere were present on GJ 1214b. Even an atmosphere composed of 99.9% spectrally neutral nitrogen with 0.1% water can be rejected on the basis of the lack of waterabsorption features.

Meanwhile, new WFC3 observations of GJ 436b presented by Knutson and colleagues point to a similarly flat and featureless transmission spectrum between 1.1 and 1.6 μm for this Neptune-class planet. Given that one might expect the more massive GJ 436b to contain more hydrogen than GJ 1214b, the flat spectrum is, in this case, an even bigger surprise — a hydrogen-rich atmosphere would be vertically extensive, and expected trace species such as water and methane would have prominent deep absorption bands. However, unlike the situation for GJ 1214b, Knutson et al. demonstrate that a hydrogen-poor atmosphere (with or without clouds) and a hydrogen-rich atmosphere with high clouds are both statistically viable solutions to explain the observed flat transmission spectrum for GJ 436b. To distinguish between these scenarios, more precise moderate-resolution spectral observations at near-infrared wavelengths will be needed to unambiguously reveal any spectral features. Longer-wavelength eclipse observations⁸, acquired when the planet passes behind the star, could also help to discriminate between the two hypotheses.

Evidence is mounting that the hydrogen

fraction within a planet is a strong function of planet size9, so it is not necessarily an 'either-or' situation for explaining the flat transmission spectra of GJ 436b and GJ 1214b: the atmospheres could be cloudy and have a large mean molecular weight. However, high-altitude clouds on these two exoplanets would not resemble the clouds we see in the Solar System. Possible candidates include potassium

chloride or zinc sulphide 'dust' clouds. For the case of a relatively hydrogen-poor atmosphere, these two components would form clouds that are optically thick (opaque) enough at high altitudes on both planets that the transmitted stellar light would be abruptly blocked, leading to a flat transmission spectrum¹⁰. Alternatively, thick hazes such as those seen around Saturn's moon Titan could be produced from photochemical processing of atmospheric gases by ultraviolet stellar photons, although the lack of evidence for methane on either of these two planets2,8 suggests that any photochemical hazes present would be decidedly different from those on Titan.

Hydrogen-poor or not, dust-shrouded or not, super-Earth and Neptune-class planets collectively represent an intriguing and populous type of extrasolar planet whose exotic atmospheres may have no true analogues in the Solar System. The transmission spectra presented here — flat and featureless, and yet full of information — provide one piece of the puzzle needed to characterize such planets. ■

Julianne Moses *is at the Space Science* Institute, Boulder, Colorado 80301, USA. e-mail: jmoses@spacescience.org

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ARCHAIC HUMANS

Four makes a party

Adding the first high-quality Neanderthal sequence to genomic comparisons of archaic and modern humans sheds light on gene flow, population structure and adaptation, and suggests the existence of an unknown group. SEE ARTICLE P.43

EWAN BIRNEY & JONATHAN K. PRITCHARD

rchaic humans have captured the popular imagination since the nine-Leenth century, when the remains of Neanderthals were discovered in the Neander valley of northern Germany and elsewhere in Europe. Until recently, Neanderthals and other archaic humans were known only from bones and various artefacts, but DNAsequencing technology is now providing us with new perspectives on these early groups

and their relationships to modern humans. In this issue, Prüfer et al. (page 43) report the first high-quality genome sequence of a Neanderthal individual. Their work adds to an emerging story about a tangled web of gene flow among modern humans and different early hominins (humans and archaic groups that are more closely related to humans than to chimpanzees), and hints at the existence of an unknown, highly diverged hominin group that contributed to this archaic gene pool.

Neanderthals are thought to have persisted

in southern Europe until around 30,000 years ago², thus potentially overlapping with modern humans. As a result, there has long been interest in whether Neanderthals might have interbred with early Europeans. In the 1990s, the first comparisons of DNA sequences from modern humans and Neanderthals^{3,4} suggested a rather simple story: that modern humans emerged from Africa during the past 100,000 years, and spread around the globe without receiving genetic contributions from hominins that had left Africa much earlier.

These early studies were based on sequences from mitochondrial DNA, which is easier than nuclear DNA to capture in ancient samples but represents only a tiny fraction of the human genome. However, the past few years have seen a revolution in our ability to obtain nucleargenome sequences from ancient samples⁵⁻⁹, and these data are providing startling insights. One surprise was the first clear evidence for interbreeding between Neanderthals and modern humans⁵; another was the discovery of a second type of archaic hominin in Eurasia in addition to Neanderthals. This group, dubbed the Denisovans, is known mainly from the genome sequence of a single finger bone found in a cave in the Altai Mountains in Siberia^{6,7}.

Although the Neanderthal bone from which Prüfer et al. derived their genomic sequence was found in the same Siberian cave, its owner is estimated to have lived several thousand years earlier than the Denisovan individual, and the two populations that the individuals represent are not closely related. The ancestors of Neanderthals and Denisovans diverged from the main human lineage about 600,000 years ago, and then split from each other around 400,000 years ago (Prüfer et al. discuss these estimates and associated caveats in detail). Thus, Neanderthals and Denisovans were quite distinct populations, having been separated for roughly three times longer than any modern human populations.

Prüfer and colleagues' sequence comparisons provide further detail about the extent of interbreeding between the different hominin groups living during the Pleistocene period (see Fig. 8 of the paper¹). The authors offer a more confident estimate of the Neanderthal contribution to the genomes of modern humans: about 2% for non-Africans (Africans have no detectable Neanderthal ancestry). They also report gene flow from Neanderthals into Denisovans that includes input at functionally important genomic regions involved in immunity and sperm function. Earlier work had shown that the main Denisovan contribution to modern humans is found in some populations in Oceania and, to a lesser extent, in east Asians^{6,7}.

Most provocatively, Prüfer et al. find evidence for modest levels of gene flow into Denisovans of sequence that is different from that of any known group, implying that there is at least one more, so far undiscovered, archaichominin group (Fig. 1). Low levels of gene flow have been observed in other radiations of species, so evidence for inter-hominin breeding should not be a tremendous surprise 10; however, it does seem that Eurasia during the Late Pleistocene was an interesting place to be a hominin, with individuals of at least four quite diverged groups living, meeting and occasionally having sex.

The Neanderthal and Denisovan genomes also share another intriguing feature: they both have extremely low genetic diversity, with only about two heterozygous sites

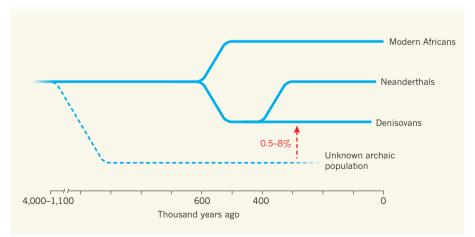


Figure 1 | Gene flow from an unknown ancient population. Prüfer et al. calculate that modern Africans show greater genomic similarity to Neanderthals than to Denisovans. Average sequence divergence along the lineage leading to modern Africans is 7.47% since the last common ancestor with Neanderthals, and 7.71% since the last common ancestor with Denisovans (both numbers represent the percentage of divergence since the human-chimpanzee split). This difference is highly significant, and is inconsistent with a simple model in which the entire Neanderthal and Denisovan genomes come from the same source population. The best alternative model identified by the authors is that there was flow of a small contribution of genomic material (0.5%-8%) into Denisovans from a highly diverged, unknown population.



50 Years Ago

The Continental Shelf Bill, which received its second reading in the House of Lords on December 3, originated in the Conference on the Law of Sea at Geneva in 1958, which resulted in the Continental Shelf Convention and the High Seas Convention. The former, which the Government intends to ratify if the Bill becomes law, clarified international law concerning those large submarine areas outside the territorial seas where the depth of the water allows the natural resources of the sea-bed and subsoil to be exploited ... In the North Sea ... Britain will have rights over any deposits up to a line half-way across to Holland, Belgium and other coastal States, subject to any adjustments resulting from the negotiations that the Government proposes to undertake after ratifying the Convention. From Nature 4 January 1964

100 Years Ago

Major H. G. Joly De Lotbinière has contributed to *The Quarterly* Review for October a valuable and timely article on the position of forestry in England and abroad, in which he reviews the principal timber resources of the world, and the steps that have been taken in England and elsewhere to provide for the future. As he points out, experts in every country are agreed that the world's supply of timber is rapidly diminishing, and that unless vigorous steps are taken in the afforestation of suitable waste lands a shortage of material must be experienced long before the close of the present century. The author indicates in a general way the lines on which the work of afforesting the sixteen million acres of mountainous and heath land in this country should be proceeded with, and urges the necessity for immediate action. From Nature 1 January 1914

(sequence differences between the paired homologous chromosomes) per 10,000 nucleotides. This equates to only around one-quarter of the genetic diversity of modern humans. The Neanderthal individual sequenced by Prüfer *et al.* had reduced heterozygosity in part because she was inbred (her parents were as related as half-siblings). However, the authors' analysis suggests that the primary cause of the low variability is that both groups had extremely small effective population sizes for the preceding 100,000 years or more.

Not only are these diversity estimates low compared with the genetic diversity of modern humans, they are also among the lowest levels of genetic diversity reported for any organism¹¹. These small population sizes seem paradoxical given the large geographical range of Neanderthals (and perhaps also of Denisovans), but they suggest that the population densities of these hominins were extremely low. Might these archaic hominins have been on their way to extinction even in the absence of any competition they may have experienced from modern humans?

The new Neanderthal genome will also provide insight into the evolution of modern humans. Prüfer *et al.* report that there are just 96 protein-coding positions at which the

Neanderthal sequence differs from that of all modern humans, with around a further 35,000 such differences at non-coding positions, some of which may affect gene regulation. This catalogue is an intriguing starting point for studying the functions of genetic differences between these groups; for example, this list is short enough to imagine creating cell lines or mouse models that contain each specific change. However, one must be mindful that many human attributes, such as bipedal gait and complex culture, probably evolved before this period of hominin diversification, and that additional important variants may lie in parts of the genome that are difficult to sequence using current methods.

After years of challenges, ancient-DNA studies are coming into their own, but they are raising as many questions as they answer. How many distinct archaic hominin groups were around in the Late Pleistocene? What were their geographical distributions? How did they help to shape the genetic make-up of modern humans? The recent sequencing of a 24,000-year-old Siberian specimen⁹ and the recovery of mitochondrial DNA from a 400,000-year-old hominin¹² are examples of how each new ancient genome adds significantly to our understanding of both recent and more distant human history. We can

expect many more exciting stories in the coming years. ■

Ewan Birney is at the European Molecular Biology Laboratory, European Bioinformatics Institute, Wellcome Trust Genome Campus, Cambridge CB10 1SD, UK. Jonathan K. Pritchard is in the Departments of Genetics and Biology and the Howard Hughes Medical Institute, Stanford University, Stanford, California 94305-5120, USA. e-mails: birney@ebi.ac.uk; pritch@stanford.edu

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CLIMATE SCIENCE

Clouds of uncertainty

An evaluation of atmospheric convective mixing and low-level clouds in climate models suggests that Earth's climate will warm more than was thought in response to increasing levels of carbon dioxide. SEE ARTICLE P.37

HIDEO SHIOGAMA & TOMOO OGURA

¬ arth is warming because of increased **◄** atmospheric concentrations of green-✓ house gases, including carbon dioxide, caused by human activities. To develop policies that can help to control anthropogenic interference in climate, estimates of climate sensitivity — the mean global temperature response to a doubling of CO₂ levels — are required, and have been sought for decades. But despite technical advances and the considerable efforts of climate scientists, the range of climate sensitivities estimated by the Intergovernmental Panel on Climate Change (IPCC) using computer models has not narrowed since 1990, and remains at roughly 1.5-4.5 °C (ref. 1). Low-level clouds occurring below 2-3 kilometres over the tropical ocean respond in various ways to a doubling of CO₂ in different models² (Fig. 1), and so are key contributors to the uncertainty of climate sensitivity. On page 37 of this issue, Sherwood et al.³

present an observational test of atmospheric convective mixing that is relevant to low-level cloud responses, and they suggest that higher climate sensitivities are more likely than lower ones.

Low-level clouds reflect incoming sunlight from space, and so cool the climate. If the amount of this cloud declines steeply as the climate warms, then more sunlight will reach the surface, an effect that contributes to higher climate sensitivity. By contrast, increases in low-level cloud result in lower climate sensitivity.

Sherwood and colleagues propose a mechanism that controls changes in the amount of low-level cloud. They reason that, as the climate warms, stronger mixing of water vapour between the low-level cloud layer and the layer of the atmosphere above it desiccates the low-level cloud layer, reducing the amount of cloud. To assess the effect of this in climate models, the authors defined and computed measures of mixing strength for 43 models that contributed

to the IPCC's fourth (2007) and fifth (2013) assessment reports.

The researchers came up with three crucial findings. First, they observed that differences in mixing strength explained about half of the spread of climate sensitivities estimated by the models. Second, they found that changes in mixing strength depend on the mixing strength in simulations of the current climate, which was used as the initial value in the experiments. And third, they conclude that estimates of current mixing strength based on observations imply a climate sensitivity of more than 3 °C, which is in the upper half of the IPCC's range of estimates.

Another recent study⁴ of constraints on the uncertainty of cloud responses, based on observational data, also suggested that higher climate sensitivities are more likely than lower ones. So can we declare the long-running debate about climate sensitivity to be over? Unfortunately not. Such sensitivity can also be inferred using observational data or using estimates of historical changes in surfaceair temperature, heat intake by the ocean or Earth's radiative balance (the heating or cooling effects of anthropogenic greenhouse gases and aerosols). One such study, published last year, implies that climate sensitivities below 2 °C cannot be ruled out⁵, demonstrating that constraints on the uncertainty depend on the approaches used to determine them.

There are many factors that could explain the discrepancy. Although the uncertainty