Eocene global warming
Hydrothermal vents prompt methane release

Malaria parasite
Hosts orchestrate antigenic variation

Photonic crystals
Perfecting the defects

Galapagos giant tortoise
Septuagenarian male seeks mate
Release of methane from a volcanic basin as a mechanism for initial Eocene global warming

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A 200,000-yr interval of extreme global warming marked the start of the Eocene epoch about 55 million years ago. Negative carbon- and oxygen-isotope excursions in marine and terrestrial sediments show that this event was linked to a massive and rapid (~10,000 yr) input of isotopically depleted carbon 1,2. It has been suggested previously that extensive melting of gas hydrates buried in marine sediments may represent the carbon source 3,4 and has caused the global climate change. Large-scale hydrate melting, however, requires a hitherto unknown triggering mechanism. Here we present evidence for the presence of thousands of hydrothermal vent complexes identified on seismic reflection profiles from the Voring and Møre basins in the Norwegian Sea. We propose that intrusion of voluminous mantle-derived melts in carbon-rich sedimentary strata in the northeast Atlantic may have caused an explosive release of methane—transported to the ocean or atmosphere through the vent complexes—close to the Paleocene/Eocene boundary. Similar volcanic and metamorphic processes may explain climate events associated with other large igneous provinces such as the Siberian Traps (~250 million years ago) and the Karoo Igneous Province (~183 million years ago).

A huge magmatic complex of dominantly subhorizontal sheets (sills) of basaltic composition intruded the Cretaceous Voring and Møre basins before, and during, the northeast Atlantic continental break-up about 55 million years (Myr) ago 5–7. The sill complex covers an area of at least 80,000 km² (Fig. 1), but sills are also likely to be present in basin segments covered by lava flows that inhibit deep imaging (for example, beneath the 13,000 km² large ‘Inner Flows’ region). The thickness and number of sills is difficult to map as subsill seismic imaging is often poor. However, both field and seismic data commonly reveal several levels of sill intrusions 8,9,10. Three sills were drilled by the well 6607/5-2 with thicknesses of 2, 91 and >50 m (refs 6, 10). The middle sill is very well imaged on seismic reflection data, and can be followed for >50 km into the Voring Basin. A conservative estimate of the volume of the sill complex in the Voring and Møre basins is 9.5–2.5 × 10⁶ km³ on the basis of an intruded area of 85,000 km² and an average vertical accumulated sill thickness of 100–300 m. The area of the entire sill complex in the North Atlantic Volcanic Province (NAV) is probably at least five times greater than the sill complex in the Voring and Møre basins. This estimate is based on the fact that the two studied basins comprise only 10% of the length of the northeast Atlantic volcanic margins, and a conservative estimate of the width of the NAV sill complex being 50% of the width of the Voring and Møre basins sill complex.

We have identified and characterized 735 hydrothermal vent complexes in the Voring and Møre basins (Figs 1, 2 and 3). The total number of complexes in the Møre and Voring basins is estimated to be at least 3–5 times greater, given the size distribution of the vent complexes and the seismic line coverage. This factor has
been confirmed by comparing the number of vent complexes identified on two- and three-dimensional (2D and 3D) seismic data in the same region. The hydrothermal vent complexes represent pipe-like structures with upper parts consisting of craters or mounds. Geochemical and petrographic data from the Voring Basin and the Karoo Basin in South Africa show that vent complexes are affected by hydrothermal fluids (ref. 14 and Methods). Hydrothermal vent complexes are interpreted to originate in contact aureoles around sill intrusions, and formed by explosive release of fluids and sediments shortly (tens of years) after sill emplacement.

Constraints on the timing of magma emplacement, and thus vent complex formation, can be obtained from seismic interpretation and biostratigraphy. The seismic interpretation reveals that the intrusive volcanism occurred mainly before the main extrusive events because: (1) the Top Palaeocene horizon (the stratigraphic level where >95% of the hydrothermal vent complexes terminate) continues beneath the extrusive Inner Flows; and (2) no hydrothermal vent complexes have been identified within or above the extrusive sequence (Fig. 1). Careful interpretation shows that most vent complexes terminate at the same stratigraphic level, the Top Palaeocene, except for 20 vent complexes in the Møre Basin that terminate within the Palaeocene sequence.

New biostratigraphic dating of the hydrothermal vent complex drilled by 6607/12-1 (Fig. 3) shows that this vent complex was formed during the TP5a palynozone (55.0 to 55.8 Myr ago), most probably at the start of the initial Eocene thermal maximum (IETM). This interpretation is based on the presence of abundant immature Apectodinium augustum palynomorphs in a 25-m interval above the lower contact of the ‘eye’ structure and a few in situ mature A. augustum palynomorphs just below this interface. The increase of A. augustum is consistent with a worldwide increase of A. augustum during the IETM, whereas the mature palynomorphs suggest a local heating event related to the formation of the hydrothermal vent complex that occurred just before the A. augustum bloom. Note that our timing is consistent with the timing of sill emplacement in the Faeroe–Shetland Basin obtained from seismic interpretation and biostratigraphic dating.

Both field and seismic data suggest that the major part of the sill complexes were formed in a short time span. Individual sills in the NAVP may be up to hundreds of kilometres long and must have formed very rapidly (tens of years) to avoid solidification. Seismic observations indicate that a small number of large-volume intrusive episodes have formed the entire intrusive complex of the Voring and Møre basins. For comparison, single flows with volumes exceeding 2,000 km³ have been estimated in the Columbia River Flood Basalt Province (that is, 4 to 12 such events may form the entire Voring and Møre basins sill complex), but even larger individual events can be expected in the much more voluminous NAVP.

Our hypothesis of a rapid melt emplacement is further corroborated by volcanological arguments. The flux of melts into sedimentary basins is ultimately controlled by the rate of melt extraction from the mantle source. A conservative estimate of the vertical mantle melt flux is 0.005–0.1 m yr⁻¹. This figure is obtained by assuming that melt is produced by 5–10% partial melting, caused by...
decompression of mantle, that rises at a velocity of 0.1–1 m yr\(^{-1}\) (ref. 19). The calculated flux range is consistent with the flux obtained from observational data in the NAVP\(^{25}\) (average melt flux of 0.0064 m yr\(^{-1}\), assuming that two-thirds of the melt volume was emplaced in 500,000 yr). The flux rates show that it will take 1,000–60,000 yr to produce the observed 100–300-m-thick sills complex without any focusing of mantle-derived melts.

The sills in the Møre and Voring basins were mainly intruded into organic-rich Cretaceous and Palaeocene mudstones\(^{16,18}\). The organic carbon is partly converted into methane when sedimentary rocks are heated beyond the gas window (\(-100–200^\circ\text{C}\); ref. 21). Accord-
ingly, the methane production potential of an intruded sedimentary basin can be estimated from the total organic carbon (TOC) content of the sedimentary sequences and the volume and thermal history of the rocks heated by the intruding sills. We define a ‘contact metamorphic aureole’ as the volume of rocks heated beyond 100°C following the sill emplacement. As a rule of thumb, the thickness of the metamorphic aureole is comparable to, or greater, than the sill thickness on both sides of thick (>50 m) sills intruded into shales\(^{6,22,23}\). The thermogenic methane produced from organic material in contact aureoles has a depleted carbon isotope ratio (\(\delta^{13}\text{C} = -35 \text{ to } -50\%\))\(^{14}\).

From Fig. 4 we estimate that 0.3 to 3.0 \(\times 10^{19}\) g of methane was produced in the metamorphic aureoles in the Voring and Møre basins just after the sill emplacement. The methane production in the entire NAVP is possibly five times higher. It has been estimated that a release of 1.1 \(\times 10^{18}\) g of CH\(_4\) (\(\delta^{13}\text{C} = -60\%\)) is sufficient to cause the \(>2.5\%\) negative excursion in carbon isotopes during the IETM\(^{1}\). Mass-balance calculations show that rapid release of the thermogenic methane produced in the metamorphic aureoles in the Voring and Møre basins (0.3–3.0 \(\times 10^{18}\) g CH\(_4\)) results in a carbon isotope excursion of \(-0.2\) to \(-3.0\%\) in the (present-day) exchangeable carbon reservoir (see ref. 3). Correspondingly, the minimum excursion resulting from methane release in the entire NAVP is \(-1.0\%\).

Recent work indicates that surface temperatures across all latitudes rose by 6 to 8°C during the IETM, implying a rapid and massive release of carbon to the atmosphere\(^{24}\). Extrusive volcanism accompanying and following the intrusive activity may have led to the release of vast amounts of greenhouse gases and aerosols in the NAVP (about \(10^{22}\) g CO\(_2\))\(^{25}\). However, the extrusive phase took place over a 2–3-Myr period, leading to average fluxes of only \(10^{13}\) g CO\(_2\) yr\(^{-1}\). Melt intruded into organic-rich sedimentary basins may cause considerably higher carbon fluxes into the atmosphere than a similar volume of erupted magma. Degassing of one cubic metre of CO\(_2\)-saturated basaltic melt may release about 3.6 kg of carbon\(^{26}\), whereas a melt intruded into organic-rich mudstones may trigger the release of 25–100 kg of carbon per cubic metre of magma. Hence, the carbon flux into the atmosphere would easily be more than an order of magnitude higher if the melt intruded into a relatively organic-rich sedimentary sequence rather than being erupted and degassed at the surface.

Contact metamorphism of organic material and associated methane venting in NAVP has the potential to cause the IETM \(\delta^{13}\text{C}\) excursion if the methane is transported to the ocean or atmosphere. Our data suggest that the observed hydrothermal vent complexes represent efficient pathways for vertical fluid transport in sedimentary basins. In addition, gas from accumulations higher in the stratigraphy could be released when pierced by the

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**Figure 3** Schematic line drawing of a seismic profile across the hydrothermal vent complex drilled by 6607/12-1. A vertical zone of disturbed seismic data is interpreted as a conduit zone connecting the tip of a sill intrusion with the palaeo-surface. The eye-shaped structure represents the upper part of the complex, probably formed by filling of an explosion crater. Similar relationships between sills, conduit zone and palaeo-surface deposits are observed in most of the >700 hydrothermal vent complexes identified in the Voring and Møre basins. Seep deposits above the eye shows that the vent complexes may be re-used for fluid migration a long time after their formation.

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**Figure 4** Estimated methane production potential of the Voring and Møre basins. This is plotted as a function of the volume of the metamorphic aureole, \(V_A\), and the amount of carbon transferred to methane, \(F_C\). The mass of methane, \(W_{\text{CH}_4}\), produced in a contact metamorphic aureole is:

\[
W_{\text{CH}_4} = 1.34 F_C V_A \rho
\]

where 1.34 is the atomic weight conversion factor between carbon and methane, and \(\rho\) is the rock density (\(\rho = 2,400 \text{ kg m}^{-3}\)). The range of \(V_A\) is based on the mapped extent of the sill complex (85,000 km\(^2\)) and an average integrated vertical aureole thickness of 200 to 600 m. A realistic range of \(F_C\) is 0.5 to 2.0 wt % (see Methods). An estimate of the amount of gas ultimately produced from the original organic carbon during maturation and metamorphism is 50–90%, depending on the kerogen type\(^{21}\). Finally, note that we have not included the possible contribution from sediment decarbonation reactions, magma degassing, or shallow gas reservoirs pierced by the hydrothermal vent complexes.
hydrothermal vent complexes. Methane erupted beneath the sea from the hydrothermal vent complexes will probably reach the atmosphere. This is supported by numerical modelling showing that rising methane plumes formed by subaqueous gas eruptions provide efficient means of transporting methane through the water column without being dissolved or oxidised.

The seismic and biostratigraphic data strongly suggest a temporal correlation between the sill emplacement and the IETM, but the data do not have the ~10,000-yr resolution required to firmly establish this link. However, this could be proved by coring the Palaeocene–Eocene boundary strata on the flanks of one or more hydrothermal vent complexes, and identifying the negative carbon isotope excursions and its relation to deposits from the vent complexes.

We conclude that explosive release of metamorphic thermogenic methane during the intrusive phase of NAVP may have caused the extraordinary warming during the IETM. For reference, the average anthropogenic release of carbon during the 1990s was 6.3 × 10^11 g carbon per year (ref. 28), which corresponds to a release of all the produced metamorphic CH₄ in the Voring and Møre basins during a period of 35–360 Myr.

Our observations stress the link between large igneous provinces (LIPs) and global climate changes. The climate impact of a LIP may be considerable if the melt is partly or completely emplaced into carbon-rich sedimentary sequences. Volcanic basins thus provide a setting for rapid perturbations of the otherwise steady release of carbon from the sedimentary reservoirs. Several other major LIPs temporally correlated with prominent negative carbon isotope anomalies contain extensive subvolcanic intrusive complexes in carbon-rich sedimentary sequences, including the Siberian Traps (~250 Myr ago; the Permo-Triassic boundary), and the Karo I igneous Province (~183 Myr ago; the Early–Middle Jurassic boundary) (compare with ref. 29).

Methods

The seismic interpretation was done on a comprehensive seismic database consisting of more than 150,000 km of high-quality industrial multichannel seismic data and one 2,000 km² 3D seismic survey using the Kingdom Suite seismic interpretation software. High-pass-filtered Bouguer gravity data and high-resolution aeromagnetic data were also loaded in the workstation project, and used to constrain the seismic interpretation. The basin models were carefully interpreted on the basis of seismic characteristics, in particular high reflection amplitude, anker shape, local transgressive segments, and abrupt reflection termination. The interpretation was corroborated by analysis of potential field data and local pre-stack analysis of the seismic data, including re-processing and modelling. The sill complex interpretation was tied to well 6607/5-2, which penetrated three sill intrusions.

The hydrothermal vent complexes were similarly interpreted using seismic characteristics. The vent complexes are characterized by a circular eye-shaped, dome-shaped or crater-shaped upper part and a chimney-like lower part with disturbed seismic character commonly surrounded by inward-dipping reflections and bright reflections19–21. Seismic evidence of fluid migration is commonly located in sedimentary strata above the vent complexes, such as chimneys, mounds, bright spots and flat spots. The disturbances sometimes continue all the way to the present sea floor. The location, size and seismic characteristics of each interpreted hydrothermal vent complex have been carefully described and stored in an electronic database. The seismic interpretation and mapping has been conducted in parallel with fieldwork on the intrusive and hydrothermal vent complexes in the Karo Basin and numerical modelling studies of formation of hydrothermal vent complexes22. The well 6607/12-1 was drilled 2 km into the centre of a hydrothermal vent complex in 1986, and provides a unique opportunity to describe and analyse the properties of a vent complex. We have completed a comprehensive study of the seismic data, wireline log data, and core data and cuttings from this well. Samples (139 in total) were collected and analysed by scanning electron microscope and microprobe, X-ray diffraction (104 samples), isotope analysis (carbon, oxygen and strontium; 76 analyses), organic geochemistry (Rockhval and total organic carbon; 67 samples), and vitrinite reflectance (78 samples). In addition, the biostratigraphy of the well was re-analysed, with particular focus on accurate dating of the Palaeocene and Eocene sequences. The data are partly described in ref. 12. Vitrinite reflectance data strongly suggest that the conduit zone of the hydrothermal vent complex is affected by hydrothermal fluids. The conduit zone is characterized by vitrinite reflectance values of up to 4.3% Ro, where 9% Ro is the vitrinite reflectance, compared with background values in the range 0.2–0.3% Ro.

Limited data on total organic carbon (TOC) values and kerogen type are published in the Voring and Møre basins. TOC values in Upper Cretaceous sediments in wells 6607/2-3, 6506/12-5 (Fig. 1) range from 0.4 to 2.6 wt % (mean = 1.4; standard
of malaria infections, when the parasite (Plasmodium falciparum) is replicating inside red blood cells. The parasite then causes an infected blood cell to rupture and release the newly developed merozoites (Fig. 1), which infect other red blood cells. (Synchronous rupture is responsible for the periodic fevers that characterize malaria infections.) Unlike most of the cells in the body, red blood cells do not carry MHC class I proteins on their surface. The merozoites replicating within the cells are therefore not subject to immune surveillance by cytotoxic T lymphocytes. However, a parasite in an infected blood cell is susceptible to being cleared (as are ageing blood cells) as it passes through the spleen. To counter this risk, the parasite inserts PEMP1 receptors into the surface of the blood cell; this facilitates binding to capillaries and delays passage through the spleen. The PEMP1 receptors are thus the major target for antibody-mediated immune responses, and have consequently evolved to undergo antigenic variation during the course of the infection.

The model\(^2\) can explain a number of epidemiological puzzles — for example, that the duration of malaria infection is longer in older than in younger children — as well as accounting for the delayed expansion of different antigenic variants despite the very high antigenic switching rate (which might otherwise be expected to result in nearly synchronous expression of the variants)\(^3\).

But Recker et al. have not yet compared the predictions of their model with other models of antigenic variation\(^4,5\).

Much remains to be done before we understand the dynamics of the merozoite stage of malaria infections. A prime task is to combine models of antigenic variation with those that allow for the effects of anaemia (caused by rupture of infected blood cells)\(^6,7\) and fevers\(^3\), and to estimate the relevant parameters from experimental data. Different models for the dynamics of antigenic variation must be compared, and we also need a better quantitative understanding of the immune responses elicited by the pathogen — in particular, why certain antigens elicit a greater replicating immune response\(^8,9\) and which factors are responsible for transient responses to some epitopes and for long-lasting immunomemorability of others.

Recker and colleagues’ model\(^2\) is an elegant twist on our current ideas about antigenic variation in malaria. But a closer interplay between different models and carefully designed experiments (perhaps using malaria-infected laboratory mice) will be essential in finding the route forward.

Hydrocarbon-driven warming
Gerald R. Dickens

A dramatic historical episode of global warming seems to have been driven by the release of huge amounts of hydrocarbons. New evidence for what might have happened comes from the sea floor off Norway.

The outstanding examples of intense global warming and massive greenhouse-gas emissions occurred during a brief episode, known as the ‘initial Eocene thermal maximum’ (IETM), about 55 million years ago. Superimposed on already warm climates, Earth’s surface temperatures soared by 5–10 °C within a geological instant\(^1,2\). At the same time, an enormous amount of carbon dioxide, apparently produced through oxidation of hydrocarbons, rapidly entered the global carbon cycle\(^3\). Scientists have only reluctantly taken the IETM as an analogue for examining our planet’s future, however, because direct evidence for the actual release of hydrocarbons, and the driving mechanism, has remained elusive.

This will change if the observations and ideas of Svensen and colleagues\(^4\) (page 542 of this issue) prove to be correct.

There is seemingly incontrovertible evidence of the injection of huge amounts of organically derived CO\(_2\) during the IETM. Numerous isotope records, constructed using data from primary carbonate or organic matter, display an extraordinary drop in the ratio of $^{13}$C to $^{12}$C at that time, clearly signalling a perturbation of the entire carbon pool on Earth’s surface\(^3\). Given the coeval dissolution of deep marine carbonate\(^3,4\), and the short duration of the isotope excursion (<20,000 years\(^1\,\)\(^5\)), at least 1,500 gigatonnes of carbon as CO\(_2\) must have suddenly been injected into the ocean or atmosphere.
Atlantic sediments where the chemical evidence for such an event is strongest. However, other than sediment slumping along the North American margin, which might be explained by processes other than gas release, no such evidence has been forthcoming. There are also problems with identifying a plausible environmental trigger for hydrocarbon release from marine sediments. Alternative, but similarly unsatisfactory, explanations for the carbon input have included the impact of a volatile-rich comet or burning of expansive peat deposits. Svensen et al. have examined data from an immense seismic array that shows features lying beneath the sea floor in two large sedimentary basins west of Norway. A truly remarkable find is their identification of several hundred kilometre-scale ‘fluid-escape conduits’ that terminate in marine strata deposited around 55 million years ago. A few such structures had been previously identified in the vicinity and were interpreted as submarine igneous volcanoes. But these conduits, which are capped by craters and mounds, more closely resemble structures seen in modern sedimentary basins, where water and gas migrate from depth and spawn mud volcanoes and hydrocarbon seeps on the sea floor (Fig. 1). The simultaneous generation and release of methane by volcanic sills solves the triggering problem. But it raises an equally contentious issue. Thermogenic methane resulting from the heating of sedimentary organic carbon contains a greater proportion of 13C than does biogenic methane. So to explain the isotope anomaly, a greater amount of carbon than previously thought — more than 3,000 Gt — must have escaped. The entire world’s conventional oil and gas deposits of oil and gas today amount to about 5,000 Gt of carbon. The mechanism proposed by Svensen et al. therefore requires the instantaneous generation and release of a truly stupendous amount of hydrocarbons. An alternative possibility is that the sills released biogenic methane that
Neurobiology

A matter of balance

Martyn Goulding

The types of chemical signal that a neuron synthesizes and communicates with were thought to be genetically encoded and largely invariable. It seems, though, that if a neuron’s activity changes, so too do its signals.

Neurons use chemical signals known as neurotransmitters to communicate with each other. These molecules come in many different flavours, and the combination of flavours used by any given neuron represents a key property that determines not only its function within a circuit, but also the circuit’s overall output. How exactly neurons regulate the profile of neurotransmitters that they express — their neurotransmitter ‘phenotype’ — is poorly understood, although it is known that most neurons synthesize a highly restricted repertoire of neurotransmitters, and that the regulatory events governing this repertoire occur in the embryo, soon after a neuron is born and begins to take on a particular identity. Numerous studies have also led to the view that a neuron’s transmitter phenotype is tied closely to the genetic programme that controls its developmental fate, such that a neuron’s identity and its neurotransmitter profile are inextricably interwoven.

On page 523 of this issue, however, Borodinsky and colleagues challenge this view. These authors provide evidence that, in the spinal cord of developing frogs, profiles of neurotransmitter expression can change in response to differing degrees of neuronal activity. Although it was well known that neurons can alter the levels of expression of particular neurotransmitters after changes in circuit activity, what is interesting about the new study is that it shows that embryonic spinal-cord neurons can also alter the types of neurotransmitter that they produce — and that they do this independently of changes in cell identity. Moreover, these changes in neurotransmitter phenotype, which seem to be encoded by the patterns of Ca2+ spikes — a measure of activity — that the neurons produce, occur in a system that was thought to be genetically ‘hardwired’.

Previously, patterns of Ca2+ spikes were shown to modulate the expression of neurotransmitters in vitro. Borodinsky et al. have now taken an elegant approach to assessing the role of Ca2+-dependent activity in neurotransmitter expression in vivo. First, they noted that different populations of embryonic neurons exhibit distinctive patterns of Ca2+ spikes. Then they studied the effects of experimentally manipulating this activity, by engineering the developing spinal cord to overexpress one of two types of ion channel: a potassium channel that hyperpolarizes neurons and so reduces Ca2+ spike activity, or a sodium channel that increases the frequency of spike activity. By injecting messenger RNA transcripts encoding one of these channels at the two-cell stage of embryonic...