

precipitation of other sulphide minerals that grew to coarser grain size. Minerals nucleated on replaced bacteria include sphalerite, galena, chalcopyrite and proustite.

The bacteria are uniformly overgrown by a coating 30–60 μm thick of amorphous silica with faintly visible concentric laminations. The silica encapsulation mimics the bacterial morphology (Fig. 1c), making the filamentous mats easily visible under low magnification (Fig. 1b). Similar coatings of amorphous silica overgrowth and cement barite crystals and altered volcanic-rock fragments throughout the hydrothermal crusts.

The silica that encloses the bacterial filaments also contains two- and three-phase fluid inclusions. No fluid inclusions were observed in the ubiquitous amorphous silica matrix of the crusts away from encapsulated bacteria. Most inclusions are spherical and 1–3 μm in diameter (Fig. 2c, d). The inclusions are filled with a yellow liquid and contain vapour bubbles, which we estimate form 2–10 vol% of the inclusions. Some appear to have small, irregularly shaped, transparent solid inclusions. Larger ($\approx 15 \mu\text{m}$), irregularly shaped fluid inclusions contain similar ratios of yellow fluid and vapour, but do not have included solids. Some larger inclusions also contain a clear fluid phase, between the inclusion wall and the yellow fluid. We interpret the fluid inclusions to be spheres of yellow hydrocarbon, formed by thermogenic destruction of bacteria, and hydrothermal fluid trapped during deposition of amorphous silica. Liquid-hydrocarbon-bearing inclusions identical in appearance to those described above have been found in hydrothermal silica deposited at sea-floor hydrothermal sites in the Guaymas Basin¹².

The fossilized bacterial mats in the hydrothermal crusts are the site of silver mineralization in these samples, but the rock record cannot define the unique role of biochemical processes in concentrating silver. Bacterial mats have been observed to form on hydrothermal deposits through which there is a diffuse flow of low-temperature hydrothermal fluid ($<35^\circ\text{C}$)¹³. Enrichment of precious metals in submarine sulphide deposits also occurs in the outer, cooler ($<300^\circ\text{C}$) parts of the deposits owing to changes of fluid chemistry (such as f_{S_2} – f_{O_2} , where f is fugacity) induced by conductive cooling and mixing with cold sea water in the near-surface environment of hydrothermal vent discharge^{14,15}. The Sea Cliff bacterial mats may serve only as nucleation sites for precipitation of sulphides from hydrothermal fluids enriched in silver. Two observations suggest a more direct biogeochemical control on silver mineralization. First, silver minerals are only found in bacterial mats, and are not associated either with sulphide fragments in the crusts or with sulphide precipitated with the silica and barite that form the matrix of the crusts. Second, the bacterial filaments seem to be selectively replaced by chalcopyrite and proustite–pearceite, and are not observed to be replaced by associated sphalerite or by pyrite, even though sphalerite occurs as overgrowths nucleated on replaced bacteria and pyrite is the most abundant sulphide mineral in the crusts.

Experiments show that bacteria can efficiently remove silver from solution by concentration and precipitation on and within cell walls¹⁶. Biochemical concentration and segregation of elements such as Ag, As and Cu in bacterial organic matter may locally concentrate these metals to a level that exceeds the solubility of their sulphides, causing nucleation of chalcopyrite and proustite–pearceite and eventual replacement of the bacterial filaments by these minerals. Alternatively, the bacterial mat may influence physicochemical parameters to favour deposition of metal sulphide minerals from hydrothermal solution. For example, facultatively autotrophic, base-producing bacteria are common in enrichment cultures from hydrothermal vent sites⁹. A bacterially mediated increase of the pH in the micro-environment of bacterial mats may lead to deposition of metal sulphide minerals owing to decreased solubility at higher pH¹⁷.

We suggest the following sequence of events, all occurring within a few centimetres of the rock/sea water interface. Initial

low-temperature venting of hydrothermal fluid allowed colonization of bacterial mats on the surfaces of fragmented basalt in contact with oxygenated sea water. The bacteria concentrated Ag, As and Cu, eventually leading to the selective replacement of bacteria by chalcopyrite and proustite–pearceite. An apparent increase in fluid temperature, probably through decreased mixing of hydrothermal fluid with sea water owing to mineral precipitation, increased the precipitation of sulphide minerals, including some chalcopyrite, sphalerite and galena, which nucleated on the replaced bacteria and grew into the open space between bacterial filaments. This increased temperature also thermally degraded the bacterial mats, producing thermogenic hydrocarbon. Continued reduction of fluid flow allowed more conductive cooling of the fluid, resulting in extensive deposition of amorphous silica¹⁸, which trapped the hydrocarbon in fluid inclusions and encapsulated the bacterial mats and their sulpho-salt-replaced filaments. □

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Comet dust as a source of amino acids at the Cretaceous/Tertiary boundary

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LARGE amounts of apparently extraterrestrial amino acids have been detected recently in rocks at the Cretaceous/Tertiary (K/T) boundary at Stevns Klint, Denmark¹. The amino acids were found a few tens of centimetres above and below the boundary layer, but were absent in the boundary clay itself. If one supposes that these compounds were carried to the Earth by the giant meteorite thought to have impacted at the end of the Cretaceous^{2,3}, some puzzling questions are raised: why weren't the amino acids incinerated in the impact, and why are they not present in the boundary clay itself? Here we suggest that the amino acids were actually deposited with the dust from a giant comet trapped in the inner Solar System, a fragment of which comprised the K/T impactor. Amino acids or their precursors in the comet dust would have been swept up by the Earth both before and after the impact, but any conveyed by the impactor itself would have been destroyed. The observed amino acid layers would thus have been deposited without an impact.

Zhao and Bada¹ listed several observations in support of an extraterrestrial origin for the amino acids they detected. The two amino acids detected, α -aminoisobutyric acid (AIB) and isovaline, are rare in the biosphere but common in meteorites. The AIB to isovaline ratio is roughly the same at Stevns Klint as it is in meteorites. Neither is known to be an alteration product, and neither was detected in several other samples that they tested. Stevns Klint isovaline is racemic, as is generally the case for abiogenic amino acids but not for biogenic.

The AIB and isovaline were found tens of centimetres below and above the K/T boundary, but not farther from the boundary nor in the boundary clay itself (Fig. 1). By meteorite standards, the quantities of amino acid are large. Using 12 p.p.m. for AIB⁴ and 480 p.p.b. for iridium⁵, AIB/Ir in the Murchison carbonaceous chondrite is ~ 15 by mass. The total AIB content at Stevns Klint was inferred to be $\sim 5 \times 10^{-5} \text{ g cm}^{-2}$ (ref. 1) and the Ir content is $3.4 \times 10^{-7} \text{ g cm}^{-2}$ (ref. 6). The integrated AIB/Ir at the K/T boundary is therefore ~ 10 times that in the Murchison meteorite. Murchison is only a tenth as rich in carbon, hydrogen, oxygen and nitrogen (the 'CHON' elements) as small dust particles from comet Halley⁷. Although some or most of the Ir in the impactor could have escaped to space, depending on the impact velocity⁸, the integrated AIB to Ir ratio is nevertheless high, especially when one considers the fragility of a molecule of isovaline compared to that of an atom of iridium.

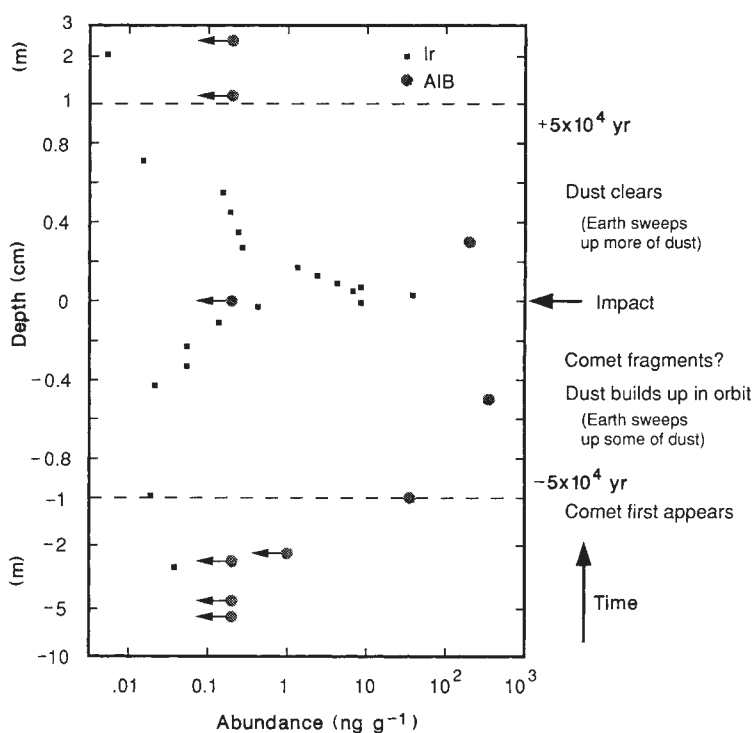
There are two objections to the hypothesis that the amino acids arrived in the impactor and later spread from the boundary clay to their present distribution. The first is that it is unlikely that a significant amount of amino acids would survive an impact of K/T scale, an impact that otherwise is only known to have been survived by elements like Ir, and for which other traces of surviving meteoritic matter (such as Xe still trapped in its high-temperature carrier) have been sought but not found^{3,9}. Incineration or atomization of the amino acids is more likely. The high temperatures and strongly oxidizing conditions in the fireball also argue against abiogenic synthesis of amino acids. The second objection is that diffusion from the boundary clay should not have left the boundary clay wholly depleted. This objection is applicable to any hypothesis that associates the amino acids with events involving the K/T impact directly.

An alternative to diffusion is to accept the sedimentary record at face value. We suggest that the extraterrestrial amino acids at Stevns Klint are cometary debris swept up by Earth, collected gently and non-destructively as interplanetary dust¹⁰. Particles smaller than $100 \mu\text{m}$ provide most of the exogenous organic material reaching Earth intact today³. Cometary dust is relatively rich in CHON elements (30%)⁷, and the particles are small enough that they would in general be expected to survive atmospheric entry intact. The comet need not have been amino acid rich, although it would support our model if it were. The interplanetary environment³ or the atmosphere¹¹ may have offered better environments for the synthesis of amino acids in dust grains than the comet. In any case, we require that comet dust contain either amino acids or their direct precursors, such as aldehydes or nitriles.

Reported deposition rates at Stevns Klint range from 1.9 cm kyr^{-1} (ref. 12) to 5 cm kyr^{-1} (above the boundary) and 12 cm kyr^{-1} (above and below the boundary, respectively)¹³. The slower rates are similar to those at other K/T boundary sites, such as Gubbio, Italy (1.1 cm kyr^{-1}) and Caravaca, Spain (3.6 cm kyr^{-1})¹². These rates are far from certain, but if they are accepted, the amino acids were deposited over 20,000 to 100,000 years. (If the amino acids were mobile, this is an upper limit.) This timescale is approximately the lifetime for evaporation of a big comet in a short-period orbit. Comet Halley, for example, is thought to be $\sim 3,000$ orbits old, having lost about 80% of its original mass¹⁴. A much larger comet could last 10^4 orbits or more. This corresponds to a lifetime of the order of 10^5 yr in a typical orbit for a short-period comet. Of course the lifetime could be shorter, especially if the comet were to disintegrate catastrophically.

Cometary evaporation could also explain the AIB profile. CHON-rich dust would have evolved from the comet over thousands of orbits before the impact. As the comet disintegrated the amount of dust in orbit increased, an increase reflected in enhanced AIB deposition. Dust remained in orbit after the impact, and so continued to be swept up for a few thousands or tens of thousands of years, a timescale consistent with its removal by Poynting-Robertson drag¹⁵. The lesser amount of AIB and isovaline above the boundary clay could be ascribed

FIG. 1 Possible interpretation of the sequence of events that occurred near the K/T boundary. Iridium⁶ and α -aminoisobutyric acid (AIB)¹ abundances near the K/T boundary at Stevns Klint, Denmark are plotted as a function of depth (mixed logarithmic and linear scales). Arrows denote upper limits. The timescale assumes a deposition rate of 1.9 cm kyr^{-1} (ref. 12).



to loss of the source. If the boundary clay was deposited quickly there would not have been time enough for it to collect much dust, which would account for the absence of amino acids. The base of the boundary clay is usually identified with direct fallout from the impact and probably was deposited quickly⁶. The bulk of the boundary clay (the 'fish clay'), however, was deposited more slowly. If deposition were slow enough, then some amino acid deposition would be expected. Arguments in favour of rapid deposition of the boundary clay are given by Kastner *et al.*⁶ and Gilmour and Anders¹⁶.

There are three difficulties with our hypothesis. The first, common to any putative extraterrestrial source, is that somehow AIB and isovaline must reach the sediments intact. Second, a high flux of comet dust is required. This difficulty is alleviated if the actual impactor were only a small remnant of an originally much larger object or one comet in a comet shower. Third, if the present AIB profile accurately records its deposition, AIB/Ir in the accreted dust must have been much higher than in meteorites. The resolution of this problem requires either an extremely AIB-rich source or segregation of Ir-bearing material from CHON-bearing dust.

Zhao and Bada¹ inferred average AIB abundances of 100 ng g⁻¹ in the sediment adjacent to the K/T boundary clay. The Ir concentration in the same sediments is ~0.02 ng g⁻¹ (ref. 6), and not obviously above background. If the Stevns Klint AIB profile accurately records the history of its deposition, AIB/Ir in our hypothetical comet dust must have been at least 5,000, which exceeds the ratio in the Murchison meteorite by 300. Either the dust was intrinsically AIB-rich or Ir-poor, or some combination of these. Taking AIB/Ir in the dust to be 300 times Murchison, and given a tenfold cometary enrichment in CHON elements and a tenfold Ir depletion (corresponding to AIB/CHON three times Murchison), for global coverage we would expect the accretion of ~7 × 10¹⁷ g of dust in 20,000 to 100,000 years. This corresponds to dust accretion rates of 2 × 10⁵–10⁶ g s⁻¹, roughly 10³–10⁴ times larger than today³.

It is reasonable to suppose that CHON-bearing dust is Ir-poor, as there is no reason to expect Ir to be found chiefly among the ices and organic molecules. It is conceivable that CHON dust was evolved or accreted preferentially. Segregation of rock and ice could be intrinsic to the comet, or a feature of cometary evolution, perhaps one peculiar to a large comet. For example, the comet may have accreted inhomogeneously, with ices precipitating on a rocky core. Iridium, a siderophile element, may have followed iron into a metallic phase that is under-represented in dust. Comets can lose volatiles preferentially; some, like Icarus or Phaethon, have evolved into asteroids¹⁷. Segregation could also stem from the relative density or strength of materials. Large meteorites (≥10⁵ g) cannot be accelerated to escape velocity from an ordinary comet by sublimating gases¹⁸. Current knowledge of the structure and composition of comets is clearly inadequate to rule out any of these possibilities.

Segregation could also be a product of orbital evolution. The much greater dust content in the inner Solar System caused by the evaporation of an enormous comet might produce a zodiacal dust regime quite different from today¹⁹. In particular, dust accretion would increase greatly if orbits were circularized by mutual collisions, thereby gravitationally enhancing Earth's collection efficiency. If CHON dust were smaller or more friable, it would be much more numerous and more subject to fragmentation and collisional circularization. To illustrate that mutual collisions can be important, we assume that Earth accreted spherical particles at the rate of $F \approx 2 \times 10^5 \text{ g s}^{-1}$. Then the mutual collision time between particles is $\tau \approx 4rp/3F$ where r and ρ are the radius and density of the particles. Taking $\rho = 1 \text{ g cm}^{-3}$, $\tau \approx 10^3 (r/100\mu) \text{ yr}$, which is shorter than the Poynting–Robertson timescale at 1 AU, ~7,000 $(r/100\mu) \text{ yr}$ (ref. 15). The total mass of a disk 1 AU in radius and 0.1 AU thick is ~10²⁰ g. If the orbits were circularized the required disk mass is reduced by the factor $(1 + v_{\text{esc}}^2/v_{\text{enc}}^2)$, where $v_{\text{esc}} = 11.2 \text{ km s}^{-1}$

is Earth's escape velocity and v_{enc} is the encounter velocity of the grains. This factor could be as large as 10.

Comets often split into pieces or otherwise disintegrate²⁰. Indeed, cometary breakup has been suggested as a way to get impact 'spikes' of 10⁴–10⁵ yr duration²¹. Extrapolation from the modern comet population implies that capture of a ~10²²-g comet into an inner Solar System orbit is a reasonably probable event over a 10⁸-yr timescale. As a very rough estimate, Encke, a comet with a 10⁴-yr lifetime, began as a ~3 × 10¹⁶ g object (Encke may be a fragment of a much larger object^{21,22}). For a cometary mass spectrum with $q \approx 1.7$ (ref. 23), a comet 5 × 10⁵ times more massive (~10²² g) might be expected over 10⁸ years. Chiron and the Great Comet of 1729 testify to the existence of comets in this general mass range. The average impact probability with Earth for a Jupiter-family short-period comet is ~1.1 × 10⁻⁹ yr⁻¹ (ref. 24). For Earth to accrete 7 × 10¹⁷ g of comet dust over 10⁵ years, the required source would need to have an initial mass of 6 × 10²¹ g. The collision of one 10¹⁸-g fragment of a 10²²-g parent with Earth is not unlikely. To illustrate, we divide the 10²²-g comet into 10⁴ equal pieces. For an impact probability of 1.1 × 10⁻⁹ yr⁻¹, 10⁴ fragments over 10⁵ yr would be expected to yield about one impact.

A comet shower, caused by a perturbation of the Oort cloud, has been suggested for the K/T boundary on other grounds²⁵, but works less well here, because a typical shower would have a timescale of ~0.8 Myr, a few times the orbital period of the dislodged comets²⁵. To reduce this to <10⁵ yr requires an encounter close enough to the Sun that most of the comets fall from inside 700 AU, a rare event expected on average only twice in the age of the Solar System²⁶. Such a shower would be extremely intense, exceeding the modern comet flux by a factor ~10⁵ (ref. 26). Olsson-Steel²⁴ conservatively estimates that long-period comets today produce one 10-km crater on Earth per 2.3 Myr. A flux 10⁵ times higher sustained for 10⁵ yr would leave 4,000 craters greater than 10 km and some 40 craters greater than 100 km. This is at least an order of magnitude too high for the K/T boundary. Because the intensity of the shower is proportional to the mass of the perturber, a brown dwarf or errant planet could in principle cause a comet shower short enough and sparse enough to match the record. If the 'missing mass' of the galactic disk is made of 0.08 M_⊙ brown dwarfs, then an encounter within 900 AU should occur in 330 Myr (ref. 27).

Our comet-dust model implies that, given equivalent preservation, the same temporal profile of AIB deposition should be seen globally. This can be tested at Stevns Klint, because the boundary clay is lenticular²⁸. A horizontally uniform distribution of AIB would support the comet-dust model, whereas a distribution correlating with the thickness of the boundary clay would support diffusion. A possible second detection of extraterrestrial amino acids at the K/T boundary has recently been reported for a site in Canada (D. Carlisle, personal communication). The amino acids at this site are reported to be located in the boundary clay itself and absent in the surrounding strata. If confirmed, this report would strengthen the case for diffusion at the Stevns Klint and would confirm amino acids as a widely dispersed phenomenon at the K/T boundary requiring non-destructive delivery. Our model also predicts that layers of extraterrestrial amino acids should be fairly frequent, although only rarely will the signal be as strong as at Stevns Klint. Because amino acid layers can form without an actual impact, these layers need not be correlated with other evidence for impact. If the dust shed by large comets frequently produced rich harvests of interesting chemicals on early Earth, and did so independently of whether the comet hit Earth, the potential for an important exogenic contribution to prebiotic organic chemistry is increased dramatically. □

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The role of disparity-sensitive cortical neurons in signalling the direction of self-motion

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MOVEMENT of an observer through the environment generates motion on the retina. This optic flow provides information about the direction of self-motion¹, but only if it contains differential motion of elements at different depths^{2,3}. If the observer tracks a stationary object while moving in a direction different from his line of sight, the images of objects in the foreground and in the background move in opposite directions. We have found neurons in the cerebral cortex of monkeys that prefer one direction of motion when the disparity of a stimulus corresponds to foreground motion and prefer the opposite direction when the disparity corresponds to background motion. We propose that these neurons contribute a signal about the direction of self-motion.

Consider an observer translating rightwards while tracking a stationary object in front of him (Fig. 1). Images of objects in the foreground (closer than the fixation point) will move to the left, while images of objects in the background (farther than the fixation point) will move to the right (Fig. 1). Without a signal indicating the depth of the two opposite motions, the direction of self-motion cannot be ascertained: the movement of the observer could equally well be to the left or the right. However, if the direction of flow could be tagged with a depth signal, the ambiguity about the direction of self-motion would be removed.

One depth signal is binocular horizontal disparity. In a frontal-eyed animal, the relative position of the images of an object on the two retinas indicates the depth of that object relative to the point of fixation. It has been proposed that the medial superior temporal area (MST) of the rhesus monkey cerebral cortex analyses optic flow^{4,5}, and we found in earlier experiments that direction-selective neurons in MST, the cells that respond to

fronto-parallel motion in one direction but not the other, carry a disparity signal. When presented with stimuli moving in their preferred direction, their discharge rate was higher when the stimuli were of one sign of disparity (for example, crossed disparities, foreground neurons) or the other (uncrossed disparities, background neurons) (J.-P.R. and R.H.W., manuscript in preparation). To test whether this disparity signal was appropriate to determine the direction of self-motion from the two opposite motions shown in Fig. 1, we presented a set of disparity stimuli moving first in the preferred and then in the non-preferred direction for the neuron under study.

We studied 65 cells. Their receptive fields were large (mean of 27° on a side, s.d. ± 12°) and often crossed the vertical meridian (57%). Of these 65 cells, 39 (60%) preferred the same sign of disparity for the two opposite directions of motion. In all these cells, however, one direction elicited a much stronger response to the preferred disparity than the opposite direction (Fig. 2a). These neurons could then detect the direction of motion of the foreground (as in Fig. 2a) or background. The relative depth signal added to the direction signal could provide information about the direction of self-motion. Under certain conditions, however, these neurons will fail to provide that information. If the observer looks at a very close object, for example, there will be only background motion, and a foreground responsive cell (such as the one in Fig. 2a) will be silent. These neurons then seem to signal the direction of self-motion only under certain conditions.

We found other neurons in MST that could play a more general part in signalling the direction of self-motion. Twenty-six cells out of the 65 tested (40%) preferred one direction of motion

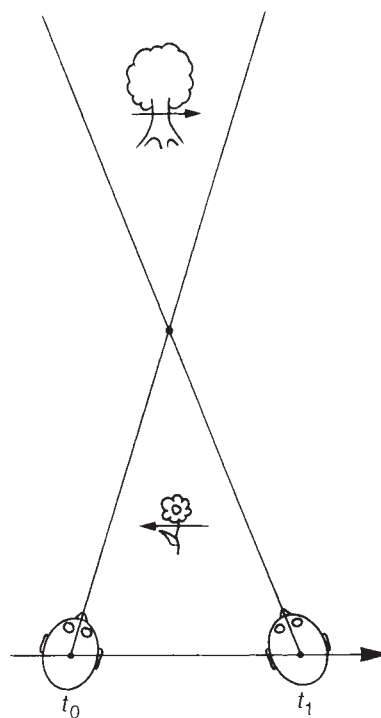


FIG. 1 Opposite motions of the background and foreground during self-motion (top view). As an observer moves to the right (large right-pointing arrow) while tracking an object, the direction of motion of the images of objects will depend on their depth relative to the point of fixation (the dot). An object in the background (behind the fixation point) 'moves' in the direction of self-motion; at time t_0 , the image of the tree is to the left of the line of gaze, at time t_1 , it is to the right relative to the line of gaze, its image has moved to the right (small right-pointing arrow). An object in the foreground (in front of the fixation point) 'moves' in the opposite direction; at time t_0 , the image of the flower is to the right of the line of gaze, at time t_1 , it is to the left; its image has moved to the left (small left-pointing arrow). These opposite motions of the background-foreground will be generated when the observer does not look in the direction of his self-motion.

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