

Faunal turnovers of Palaeogene mammals from the Mongolian Plateau

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Most orders and many families of modern mammals were established during the Palaeogene. Mammalian evolution during this period of time has been correlated with global climatic events^{1–4}, although the timing, mode and scale of such a climate–evolution link remain debatable^{1,5,6}. The Palaeogene global climate was step-punctuated by a warming across the Palaeocene/Eocene boundary about 55 Myr ago and a cool-off throughout the late Eocene and early Oligocene epochs^{1,2,7–10}. The most severe cooling was at 33.5 Myr, slightly after the Eocene/Oligocene boundary, and was characterized by a drop in the mean annual temperature and by changes in vegetation from Eocene dense forests to Oligocene more open country⁵. Here we analyse 33 Palaeogene mammal faunas from the Mongolian Plateau of China and Mongolia. There is a distinct pattern of faunal turnovers: perissodactyl-dominant faunas of the Eocene were abruptly replaced by rodent/lagomorph-dominant faunas of the Oligocene. We interpret the turnovers as having been effected by global climatic shifts and name the prominent biotic reorganization across the Eocene/Oligocene boundary the Mongolian Remodelling, which correlates to the European *Grande Coupure*.

Studies of the effect of climate on mammalian evolution have almost all been made in North America and Europe². To study Palaeogene faunal turnovers in Central Asia and their possible relationships to climatic changes, we analysed 454 species, representing 210 genera and 88 families of mammals, from 33 local faunas in the Mongolian Plateau of China and Mongolia (Fig. 1). Taxonomic names above the species level follow an updated classification of mammals¹¹. We correlated these local faunas using a numerical clustering method (see Methods) and then

converted the clustered faunas to a sequence of local mammal ages on the basis of their stratigraphic occurrences (Fig. 2). We used three radiometric datings and intercontinental faunal correlations to correlate the sequence of relative ages with the geological time-scale and boundaries¹².

In all calculations the late Palaeocene and Oligocene faunas always clustered as one group, whereas the Eocene faunas may or may not form a single group (Fig. 2; Methods), indicating taxonomic differentiations among faunas of the Palaeogene epochs. We concur with placement of the Palaeocene/Eocene boundary (PEB) between the Gashatan and Bumbanian¹³ but note the possibility that it may be above the Bumbanian¹⁴. Our reallocation of the Eocene/Oligocene boundary (EOB) at the Houldjinian/Hsandagolian transition differs from the traditional placement of the EOB between the Sharamurunian and Ulangochuan^{15,16} but agrees with the ideas of others^{1,17,18}. Our method cannot differentiate Hsandagolian faunas into the biochronological subunits described in ref. 19, reflecting the faunal stability during that period of time¹⁹. Temporal distributions of important families show that, at the PEB, several archaic taxa (such as multituberculates) became extinct (Fig. 2), whereas Artiodactyla, Euprimates, Condylarthra, true rodents, and Perissodactyla made their first appearance. The Arshantan age witnessed the second significant faunal change, characterized by appearances of several perissodactyl families. The most important biotic reorganization occurred at the EOB: many modern families belonging to rodents, lagomorphs, erinaceid insectivores, ruminant artiodactyls and carnivores first appeared. Future studies may prove the Houldjinian to be only part of the Ergilian¹⁵ and the Kekeamuan a subunit of the Hsandagolian¹⁸; the former possibility would increase the extinction rate and the latter would decrease the rate of first appearances at the proposed EOB.

The Gashatan and Bumbanian faunas consist mostly of archaic taxa, none of which show dominance (Figs 2 and 3). Despite varying species numbers among faunas, which may be biased by taphonomy and collection or may actually reflect species diversities, all other Eocene faunas are dominated by perissodactyls. The Eocene faunas were then abruptly replaced by Oligocene ones in which rodents and lagomorphs were the prevailing primary consumers, rivalling other taxa not only in species numbers but also in numbers of individual organisms (M.C.M. *et al.*, manuscript in preparation). Except for a single primate species from the Bumbanian fauna²⁰, we have not found any of the euprimates, chiropterans, and plesiadapiformes that are common in the Palaeogene of North America and Europe²¹. The

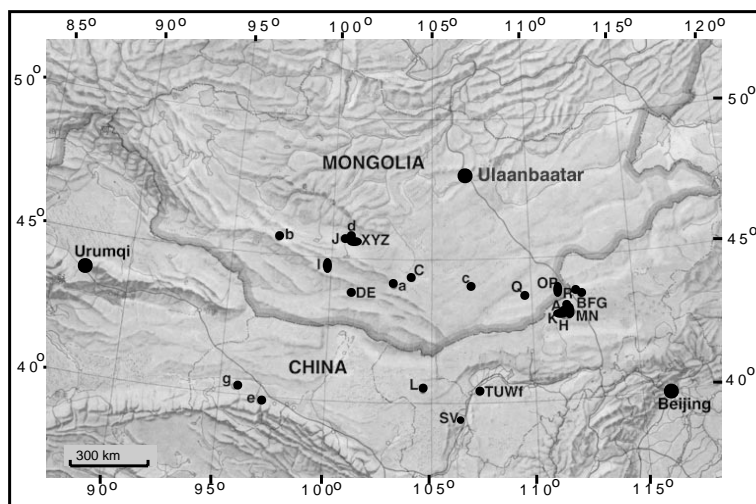


Figure 1 Location map of 33 Palaeogene faunas from the Mongolian Plateau. Faunas are: A, Nomogen; B, Bayan Ulan; C, Gashato; D, Naran; E, Bumban (Tsagan Khushu); F, Arshanto; G, Irdin Manha; H, Ulan Shireh; I, Khaychinq; J, Kholboldzhi; K, Shara Murun; L, Chaganbulage; M, Ulan Gochu; N, Urtyyn Obo; O, Sevkhul at Khoer Dzan; P, Ergilian at Khoer Dzan; Q, Ergilian Dzo; R, Houldjin; S,

Kekeamu; T, Lower Wulanbulage; U, Upper Wulanbulage; V, Ulanatal; W, Saint-Jacques; X, Ulaan Khongil (Tatal Member of Hsanda Gol Formation); Y, Ulaan Khongil (Shand Member); Z, Zavlia (Shand Member); a, Tsakhir; b, Khatan-Khay; c, Shunkht; d, Tsagan Obo; e, Shargaltein; f, Yikebulage; g, Taben Buluk.

apparent lack of these forest-related species implies the absence of dense forests in the region.

Body sizes of species are the most useful single predictor of species adaptation²² and are indicated here by tooth dimensions (Fig. 3; Methods). The Gashatan and Bumban faunas are composed mainly of small and some medium-sized species. The middle and late Eocene faunas show a significant size jump: medium- to large-sized species become common, some of which are among the largest terrestrial mammals ever known. In contrast, the Oligocene faunas experienced a size decrease: large species are few, medium-sized are rare or absent, and small mammals became dominant. The size changes correspond with those of tooth morphologies. As one of the most important groups in the Mongolian Palaeogene, rodents evolved from having a primitive tribosphenic tooth pattern in the late Palaeocene to possessing quadrate-crown molars by the Bumbanian (Fig. 4). Except *Ardynomys* of the family Cylindrodontidae, Eocene rodents have cusps, broadly basined, and low-crowned molars. The Oligocene rodents show a variety of tooth morphologies that are typical of lophodonty, some additionally evolving hypsodonty. Other Oligocene primary consumers, such as ochotonid lagomorphs and ruminant artiodactyls, also developed high-crowned teeth^{19,23}.

Thus, our results reveal a distinctive pattern of faunal turnovers that is reflected by taxonomic differentiation, species appearances and extinctions, reorganization of faunal compositions, changes of species body sizes, and evolution of rodent dentitions. In addition,

major faunal changes occur at short intervals coeval with major climate shifts and are followed by long periods of stability of new communities. Taphonomy, palaeoecology, and methods of collecting are common factors that may bias fossil assemblage data²⁴, as discussed in some studies of Mongolian taxa^{14,15} (M.C.M. *et al.*, manuscript in preparation), but these factors are unlikely to result in such consistent proportions of faunal composition and size structure for the faunas that came from different sediments of the same or different ages; nor does predation account for the onset and crash of the Eocene perissodactyl-dominant faunas. Competition may play only a minor role in shaping the turnover pattern because differences in size and functional morphology between large perissodactyls and small mammals indicate indirect competition for resource use²⁵. Unlike in the European *Grande Coupure*²⁶, the arrival of immigrants as possible competitors is not significant in the Mongolian Palaeogene. Moreover, changes apparently occur across whole faunas, not just in potentially competing lineages.

The Mongolian faunal turnovers are probably effected by major climatic changes. Faunal compositions reflect warm, humid conditions that favoured perissodactyls for most of the Eocene, and a cool, arid environment supporting rodents and lagomorphs during the Oligocene. By comparison with modern and other fossil mammal faunas^{4,27}, the presence of all sizes of species in the Eocene also indicates that Eocene conditions were humid and rich in vegetation, whereas the lack of medium-sized species in the Oligocene indicates that environments were open and arid. In

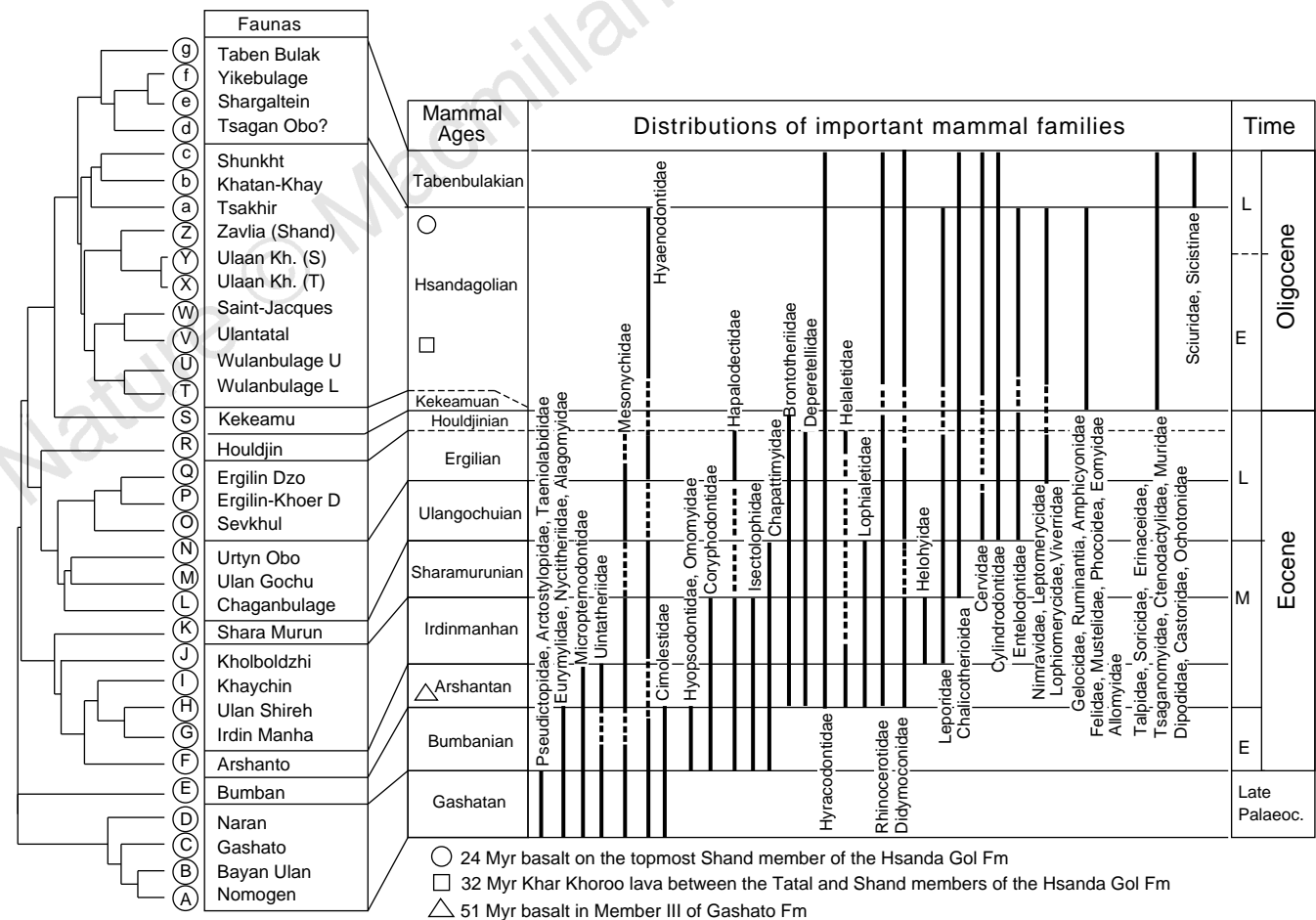


Figure 2 Correlation of local faunas by clustering (see Methods), local mammal ages, and distributions of important mammal families from the Mongolian Palaeogene. Dashed lines indicate no records. The ⁴⁰Ar-³⁹Ar datings of the Khar Khoroo Lava range from 30.9 to 33.7 Myr, whereas the basalt resting at the topmost Shand Member is dated 21-25 Myr (M.C.M. *et al.*, manuscript in

preparation). The less certain 51 ± 3 Myr dating of the basalt in the Gashato Formation is correlated by the presence of *Gomphos elkema* to the top of the Bumban Member in the Naran Bulak Formation¹³. Letters A-Z and a-g at the left relate to locations shown in Fig. 1. Letters at the right are: L, late; M, middle; E, early.

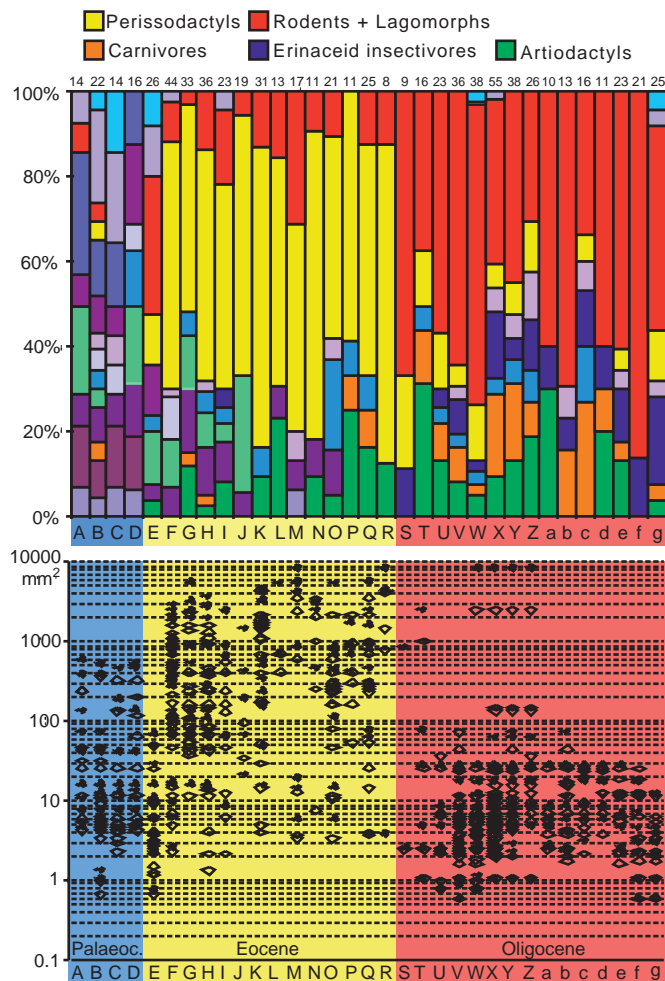


Figure 3 Changes in faunal composition and dental morphology. Top, faunal compositions (in percentages) show the predominance of perissodactyl faunas in the Eocene and of rodent/lagomorph faunas in the Oligocene (complete faunal lists are available as Supplementary Information). Numbers of species for each fauna are at the top of the columns. Bottom, \log_{10} plot of lower and upper molar areas (empty and solid diamonds, respectively; see Methods) in each fauna. We arbitrarily divided the species into three categories: small (TA (upper tooth area) $< 100 \text{ mm}^2$; roughly the size of a small deer or smaller); medium ($100 < \text{TA} < 900 \text{ mm}^2$; approximately up to the size of a tapir); and large ($\text{TA} > 900 \text{ mm}^2$; up to the size of an animal that is 8-m long and 5-m high, about four and a half times as heavy as an adult elephant). There may be biases due to different proportions of tooth-body size between Palaeogene and extant mammals²². Letters on the x-axis correspond to the faunas shown in Figs 1 and 2.

addition, the development of the lophodont and hypsodont teeth in Oligocene rodents and other herbivores probably reflects increased efficiency in grinding abrasive foods²⁸ which are more likely to be expected in arid environments. Therefore, we conclude that the nature of the faunal turnovers of the Mongolian Palaeogene supports the climate/mammalian-evolution link. This pattern is generally comparable with the global framework of mammal evolution, and contrasts with a previous convention²⁹; however, it resembles the European pattern more than the North American one because the most significant turnover in the North American Palaeogene is at the middle-to-late Eocene transition¹. We name the biotic reorganization at the EOB the Mongolian Remodelling and correlate it to the European *Grande Coupure*; both events reflect changes in the environment from a warm, humid Eocene to a cool, arid Oligocene. Because many taxa involved in the Mongolian Remodelling dispersed to Europe at the *Grand Coupure*, the beginning of the

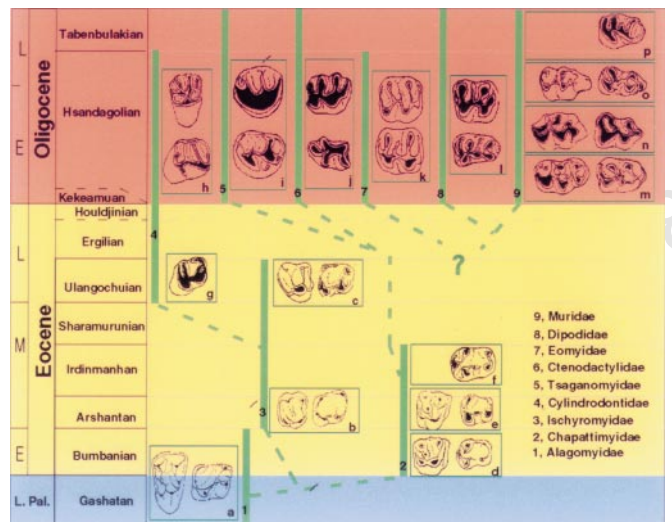


Figure 4 Morphologies of the first right upper and lower molars (anterior to the right; some are photographically reversed; not to scale) of the main Palaeogene rodent families from the Mongolian Plateau. Solid green bars represent distributions and dashed green lines are possible phylogenetic relationships. The species representing each family are: a, *Tribosphenomys minutus*; b, *Asiomys dawsoni*; c, *Hulgana ertnia*; *Sharomys singularis*; e, *Tamquammys wilsoni*; f, *Advenimus burkei*; g, *Ardynomys olseni*; h, *Anomoemys lohicolus*; i, *Tsaganomys altaicus*; j, *Tataromys plicidens*; k, *Eomys orientalis*; l, *Plesiosminthus tangingoli*; m, *Cricetops dormitor*; n, *Selenomys mimicus*; o, *Eucricetodon asiaticus*; and p, *Tachyoryctoides obrutschewi*. L, late; M, middle; E, early.

Mongolian Remodelling is probably slightly older than the *Grande Coupure*. □

Methods

We clustered faunas using multivariate analysis on an IBM PC³⁰. We used Jaccard and Dice coefficients to build similarity association matrices from binary data (presence and absence of families, genera, and species in faunas). Faunas were then clustered by the unweighted pair-group method (arithmetic average)³⁰. All data generate the main groupings shown in the generic phenogram of Fig. 2, which is the phenogram most congruent with stratigraphical occurrences of faunas. A total of 335 upper and 396 lower molar areas are plotted. Each plotted value is an average of available measurements of molars for a given species. For instance, if only M1 and M2 are available for a species, the upper tooth area is (M1 area + M2 area)/2. Each tooth measurement for a species is an average of 1–50 specimens. Most measurements are from literature, supplemented with our own data. Measurements in some taxa, either being studied or fragmentary, are not included; however, expected size distributions of the missing taxa support the plotting results in Fig. 3. Faunal lists and measurements are available as Supplementary Information.

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Supplementary information is available on Nature's World-Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature.

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Veil architecture in a sulphide-oxidizing bacterium enhances countercurrent flux

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Solute uptake by microorganisms is limited by molecular diffusion through a boundary layer surrounding the cells, and the uptake is not enhanced (or only insignificantly) by convective water transport or by swimming¹. It is generally assumed that sediment uptake of oxygen is diffusion-limited, so the steepness of the concentration gradient within the 0.5–1-mm-thick diffusive boundary layer is a measure of diffusional flux into the sediment^{2,3}. Here we show that veils, which are formed on sediments by the marine sulphide-oxidizing bacterium *Thiovulum majus*⁴, generate convective oxygen transport through the 0.5-mm-thick water layers above the veil at rates that are about 40 times higher than molecular diffusion. Chemosensory behaviour of the cells, combined with their generation of water currents, leads to characteristic, aggregated distribution patterns: areas with high cell densities draw oxygenated water downwards through the veil, whereas areas without cells serve for the upward-directed return flow of deoxygenated water. The microbial community structure thus overcomes the limitations of diffusion and thereby enhances the rates of respiration and sulphide oxidation.

Thiovulum majus forms characteristic white veils on or slightly above sulphidic sediments. The cells are unusually large (5–10 µm diameter) and they are among the fastest-swimming bacteria

known (150–600 µm s⁻¹)⁵. Their motility has both a translational and a rotational component resulting in a helicoid swimming path. The cells show a pronounced chemosensory behaviour in O₂ gradients, in which they form a narrow band at an O₂ tension of about 4% atmospheric saturation (0.85 kPa); in nature this ensures that the bacteria aggregate in a <100-µm-thick zone where oxygen and sulphide coexist^{4–7}.

An approximately 100-µm-thick band of swimming *Thiovulum* cells, maintained by a steep O₂ gradient within a glass capillary, caused no detectable displacement of suspended latex particles outside the band. Within the band, individual latex particles were displaced during close encounters with swimming cells. Among 20 such encounters, the maximum displacement (λ) recorded was 10 µm, and the duration of the displacements (τ) was 0.3–0.5 s. A crude estimate of diffusive mixing due to bacterial swimming is then given by λ²/4τ, or about 6 × 10⁻⁷ cm² s⁻¹. This value, which represents an overestimate because only a fraction of the beads were moving at any time, is much lower than diffusivity of dissolved O₂. These results accord with theoretical hydrodynamics: non-thrust swimming at low Reynolds numbers causes only a local flow field (less than the length of the translating cell), whereas tethered cells cause a large-scale flow field⁸. In addition, swimming cells should not cause a large-scale convective flow because they swim in random directions within the band⁶.

Under optimal conditions, cells secrete a mucous thread from their posterior end. The threads, which may exceed 100 µm in length, tend to attach to solid surfaces, but the cells detach themselves from the thread if the O₂ tension deviates from the optimal value⁶. Attached cells are typically oriented towards the oxic side of the chemical gradients. The cells maintain their rotational motility (with an angular velocity of ~30 s⁻¹), but translational motion is prevented by the stretched thread. Instead, the cells create a flow field with a velocity of ~200 µm s⁻¹ close to the cell (Fig. 1a).

The attached bacteria form characteristic white veils on natural sulphidic sediments. These are sometimes constituted by equally spaced cells punctuated by holes measuring 100–500 µm in diameter and with a raised rim (Fig. 2). Alternatively, the cells occur in small, regularly spaced clusters, each containing 25–100 cells (Fig. 3). The type of veil that develops is a function of the height of the O₂–H₂S transition zone above the sediment: continuous veils with more or less regular holes occur mainly over depressions in the sediment surface, whereas isolated cell clusters appear on slightly elevated areas.

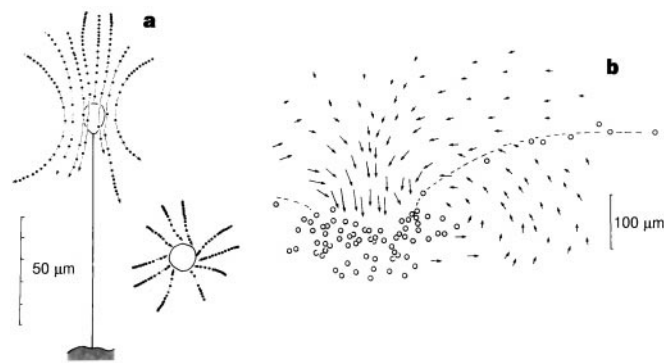


Figure 1 The flow field around *Thiovulum* cells. **a**, Flow field around two isolated and attached cells seen from the side (left) and from above (right), respectively. Time interval between positions of latex beads (black circles) is 0.04 s. **b**, Side view of the flow field (velocity vectors) around a group of attached cells; the posterior and anterior ends of the arrows indicate the positions of a bead before and after an interval of 0.2 s. The dashed line reflects the horizon where swimming *Thiovulum* cells occurred; it corresponds to an O₂ tension of approximately 4% atmospheric saturation.