in the Andes. Although changes in temperature are probably the dominant mechanism which produces this melting, there is also evidence, from both observations and models, that the changes in temperature have been accompanied by increases in moisture content in the lower tropopposphere[17,18], which is consistent with the increase of the tropical SST and the resulting enhancement of the tropical hydrological cycle. These increases in humidity would also contribute to accelerated melting rates[4].

On the basis of very long isotopic records obtained from the various tropical ice-cap cores (of the order of several centuries to several thousand years), the warmth recorded in the tropical oceans in several past decades may perhaps be at an unprecedented level since the mid-Holocene period (~3,000–4,000 yr BP)[7]. Whether this recent increase is natural, anthropogenic, or both, remains an open question. Recent evidence[1,11], however, suggests that high-elevation environments may be particularly sensitive to long-term changes in tropical SST and tropospheric humidity, which are likely to have an impact on the hydrological and ecological balances of high-altitude zones throughout the globe, perhaps to the greatest extent in the tropics. □

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Microbial generation of economic accumulations of methane within a shallow organic-rich shale

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ALTHOUGH **methane of bacterial origin is ubiquitous in marine and freshwater sediments, economic accumulations of bacterial gases occur mainly at depths of several kilometres in Tertiary basins that had high sedimentation rates[1,2]. Here we present an integration of geochemical and isotopic data from gas and water extracted from the Upper Devonian Antrim shale, along the northern margin of the Michigan basin, which demonstrates that significant volumes of bacterial gas have been generated in organic-rich shales at depths of less than 600 metres. The Antrim shale is mainly a self-sourced reservoir, in contrast to conventional gas deposits that have migrated from a source to a reservoir, and has become one of the most actively exploited gas reservoirs[3] in the United States. The gas-forming processes operating at shallow depths in the Antrim shale are not unique[4], and an understanding of these processes should lead to the identification and development of other economic, non-conventional gas deposits around the world.**

The Antrim shale is rich in organic matter (up to 20 wt%), comprised of hydrogen-rich algal material and is thermally immature (vitrinite reflectance $R_o = 0.4–0.6$) in the area of study[5]. Our study area is along the northern margin of the Michigan basin

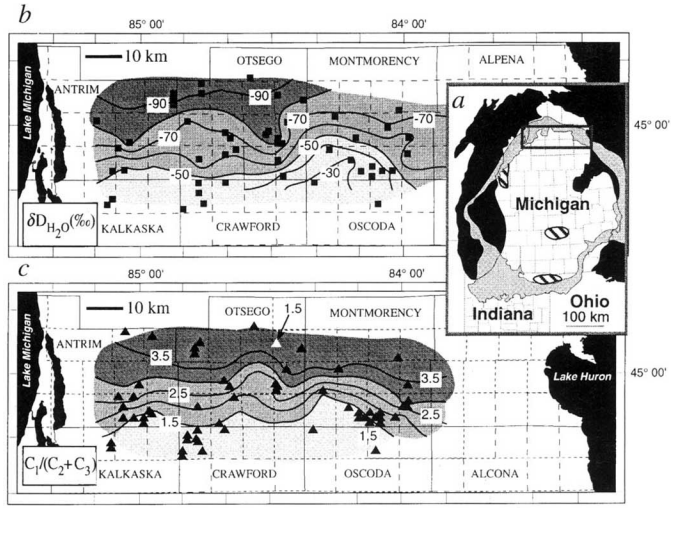

FIG. 1 *a*, Study area at the margin of the Michigan basin in northern Michigan, USA with the subcrop of the Antrim shale shown in grey. Over 5,000 wells have been completed in the shale for commercial production of methane. Of these, over 95% were commercially successful. Estimates[3] of total Antrim shale reserves for the Michigan basin are in the range $(9–29) \times 10^{11}$ m^3. Gas and co-produced water were collected at the well-head. Sampling depths ranged from 200 m on the northern margin of the producing zone, to nearly 650 m in the south. Striped areas indicate regions of new exploration. *b*, Gradients in δD values of water (shown on contours) occur over the producing trend due to freshwater ($\delta D \approx -90‰$) influx mixing with basinal brines ($\delta D \approx -30‰$). Well locations are shown as filled squares. The δD value of the water was determined using a Finnigan MAT Delta S ratio mass spectrometer, with a precision of ±2‰. Waters were reacted with zinc metal to liberate hydrogen gas[28]. *c*, A plot of $\log(C_1/(C_2 + C_3))$ for produced gas from the Antrim shale, showing a steep gas compositional gradient (with increasing C_{2+} content) from the margin towards the centre of the basin. The value for one anomalous well (shown as an open triangle) is not contoured as contamination is suspected. Gas samples were obtained from the well-head using stainless-steel cylinders, and analysed by routine gas chromatographic techniques.

(Fig. 1*a*) where the Antrim shale subcrops under a variable thickness of Pleistocene glacial drift. This region experienced multiple glacial advances and retreats[6] which greatly modified the hydrological and pressure regimes, possibly enhancing meteoric water recharge in the northern part of the basin[7]. Gas is produced from natural and enhanced fractures[8,9] within the Antrim shale. Over 5,000 wells produce 1.2×10^7 m^3 of gas per day (ref. 3), as well as large quantities of saline water. The gas is mainly composed of methane (CH_4), but also includes varying amounts of carbon dioxide (CO_2) and ethane (C_2H_6). Because most gas reserves are adsorbed within the organic shale matrix[3], gas production rates are enhanced by lowering pressure at the borehole by means of dewatering.

The origin of gaseous hydrocarbons and carbon dioxide in the Antrim shale reservoir has been uncertain. An early study suggested that gas from the Antrim shale might be of microbial origin on the basis of its high methane content and shallow depths of production[10]. Recent research favours a thermogenic origin, based on $\delta^{13}C$ values of $\sim -50‰$ (w.r.t. the VPDB standard) for methane[11]. However, the carbon isotope composition of methane by itself does not reveal its origin, as it varies directly with the $\delta^{13}C$ value of the carbon source. For example, bacterial methane generated in closed systems can have $\delta^{13}C$ values similar to that of incipient thermogenic methane (~ -60 to $-40‰$), depending on the $\delta^{13}C$ of the CO_2 which has been reduced by bacterial action[12–15].

We examined the chemical and isotopic compositions of the gas and co-produced water from the Antrim shale. The relationship between the hydrogen isotope compositions of methane and co-produced water, in conjunction with the carbon isotope compositions of both carbon dioxide and methane[16–18], suggest that the dominant source of methane in the Antrim shale is microbial methanogenesis[9]. Relatively recent water recharge induced strong isotopic and related chemical gradients over the producing trend, as illustrated by the δD values of water (Fig. 1*b*). Dilute ground water (<0.1 M NaCl: δD more negative than $-90‰$) is recharged into the Antrim shale at the subcrop through an extensive fracture network[8,9] and progressively mixes with basinal brine (>4 M NaCl; δD more positive than $-30‰$) (Fig. 1*b*).

Carbon-14 data from dissolved inorganic carbon (DIC) in water from the Antrim shale constrain the recharge age to a maximum value of 22,000 yr BP (ref. 9). Concentrations of DIC in waters produced from the Antrim shale are far greater than those of the ground waters from glacial drift. These dilute waters enter the Antrim shale with approximately 3–6 mM DIC and become charged with DIC concentrations up to 70 mM. The DIC in waters from the Antrim shale has unusually positive $\delta^{13}C$ values of approximately $+30‰$ (w.r.t. VPDB)[9] and ultimately is derived from the abundant immature organic matter present in the shale by means of microbial activity.

Direct evidence for a microbial metabolic pathway is the positive correlation of δD values of CH_4 and formation water produced from the same well. In environments similar to the Antrim shale, carbon dioxide reduction is the dominant microbial pathway[4,14,18]. This pathway involves two steps. Bacteria metabolize organic compounds and water by means of enzymatic reactions to produce hydrogen and carbon dioxide[16,19]. Experimental data suggests that the free hydrogen produced in this way exchanges with environmental water[12]. Methanogens subsequently reduce the carbon dioxide using this hydrogen. Thus, the hydrogen isotope composition of methane produced by carbon dioxide reduction is dependent on the hydrogen isotope composition of the associated water (Fig. 2*a*, solid line). Gas and water from the Antrim shale have δD values which fall near the line with a slope of unity (Fig. 2*a*), suggesting that they are largely formed via the carbon dioxide reduction pathway. In contrast, fluids sampled from the stratigraphically lower carbonates of the Silurian Niagaran formation and in deeper-producing wells from the Antrim shale, nearer the centre of the basin, clearly deviate from the trend shown for microbial gases. These gases are of thermogenic origin[20], and the hydrogen in methane has not exchanged with associated waters (Fig. 2*a*).

A microbial origin of methane from the Antrim shale is further supported by comparison to known bacterial gases from glacial drift deposits in the Illinois basin which share a similar carbon isotope fractionation between carbon dioxide and methane[14,18]. In the Illinois basin, low $\delta^{13}C$ values of CH_4 occur, indicating an open system where the supply rate of CO_2 is rapid compared to the rate of methanogenesis. In a closed or CO_2-limited system, CO_2 is progressively converted to methane and the $\delta^{13}C$ of residual CO_2 becomes increasingly more positive[13,14,18]. The CO_2 in gases from

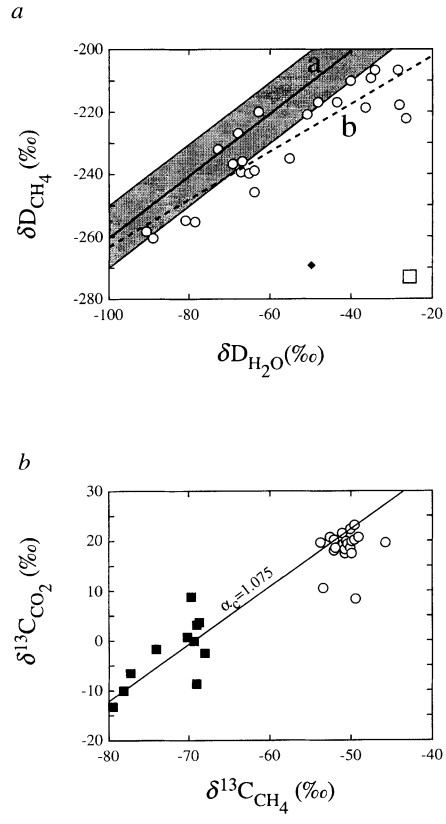

FIG. 2 *a*, Hydrogen isotopic composition of methane and associated (co-produced) water (open circles). The solid line 'a' follows the equation $\delta D_{CH_4} = \delta D_{H_2O} - (160 \pm 10)‰$ (refs 16, 19) with a slope of one (where δD_{CH_4} is the δD value of CH_4 and δD_{H_2O} is the δD value of H_2O) suggesting that all hydrogen in the methane is from water. This is consistent with microbial formation of CH_4 via CO_2 reduction ($CO_2 + 4H_2 \rightarrow 2H_2O + CH_4$). The area shaded in grey shows the variance ($\pm 10‰$) around the ideal line. The correlation of Antrim shale gas and water samples (dashed line 'b'; $y = 0.76 \times -186.71$, $r^2 = 0.80$) is evidence of microbial methane production by CO_2 reduction. Mixing with thermogenic gases would move Antrim shale gas samples off the slope of one. Thermogenic gases form one Niagaran limestone location (filled diamond) and one Antrim shale mid-basin sample (open square) are outside the bacterial population. Carbon and hydrogen isotope analyses of gas were performed using VG 903 and VG 602 mass spectrometers, respectively[29]. The δD values are given relative to the VSMOW standard, and the $\delta^{13}C$ values relative to the VPDB standard. Reproducibility for isotopic measurements are $\pm 1.7‰$ for δD and $\pm 0.1‰$ for $\delta^{13}C$. *b*, Plot of $\delta^{13}C$ values of CH_4 versus $\delta^{13}C$ of CO_2 for gases from the Antrim shale (open circles) and from gases produced microbially in the Illinois basin (filled squares)[14]. For reference, a fractionation factor (α_c) of 1.075 where $\alpha_c = (\delta^{13}C_{CO_2} + 10^3)/(\delta^{13}C_{CH_4} + 10^3)$ (suggestive of microbial processes) has been plotted[18]. Neither Silurian Niagaran formation gases nor the single Antrim shale gas sample from the central basin contain sufficient CO_2 for isotopic analysis.

the Antrim shale has $\delta^{13}C$ values up to +22‰ (VPDB). Carbon dioxide reducing methanogens metabolize this ^{13}C-enriched CO_2 and produce correspondingly positive $\delta^{13}C$ values of CH_4 (Fig. 2*b*).

The molecular composition of gases from the Antrim shale varies from pure methane to ~5 vol.% of hydrocarbons with two or more carbon atoms (C_{2+}). Virtually pure methane is produced near the basin margin, and gases with increasingly greater ($C_2 + C_3$) contents are produced deeper in the basin (Fig. 1*c*). These molecular ratio patterns are consistent with mixing, bacterial alteration or migration phenomena[21]. In general, higher-molecular-weight compounds such as ethane and propane tend to be retained in the rock, and lower-molecular-weight gases (that is methane) migrate more readily[22]. Mixing of two thermogenically sourced gases of differing thermal maturity could produce the $C_1/(C_2 + C_3)$ ratios observed, but should result in a shift of $\delta^{13}C$ values across the study area[15,16]. The $\delta^{13}C$ values of CH_4 from the Antrim shale, however, show no coherent regional pattern (Fig. 3*a*). Diffusive migration can be ruled out because methane in the north has a different δD value from methane in the south, and fractionation of only one isotopic species is unlikely. Importantly, $\delta^{13}C$ values of ethane and propane (M.S. and A.M.M., unpublished data) increase with proximity to the subcrop. This pattern is consistent with bacterial oxidation, probably occurring during the initial influx of meteoric water at the subcrop. This process is not volumetrically significant as $\delta^{13}C$ values for methane do not increase at the subcrop of the Antrim shale[23] (Fig. 3*a*). Significantly, bacterial oxidation of a thermogenic gas would not produce the observed correlation between δD values for water and methane.

We suggest that the gas in the Antrim shale originates from the mixing of thermogenic gas (with $C_1/(C_2 + C_3) < 100$) and methane of microbial origin having similar $\delta^{13}C$ values of methane (Fig. 3*b*). Plausible sources for the thermogenic gas endmember are the Silurian Niagaran formation or the mid-basin Antrim Shale. Methane in gases from the Niagaran formation have $\delta^{13}C$ values of approximately −51‰ and $C_1/(C_2 + C_3)$ ratios from 2 to 10. Gas produced from the Antrim shale in the middle of the basin has a $\delta^{13}C$ value of −54‰, a $C_1/(C_2 + C_3)$ ratio of 9, and CO_2 content too low to measure. These findings suggest that both gases are thermogenic in origin[15,16,24]. Thus, variations in the concentration of C_{2+} hydrocarbons near the subcrop occur owing to a combination of bacterial oxidation and mixing of thermogenic and microbial gas (Fig. 1*c*).

Extensive microbial methanogenesis at shallow depth has important implications for the timing of water recharge and methane generation in the Antrim shale. The δD values of methane and co-produced water from the Antrim shale require that the waters have a residence time greater than that needed to generate the significant methane accumulation. This microbial gas generation in the Antrim shale occurred during or following the final stages of Pleistocene glaciation in northern Michigan based on ^{14}C ages of DIC in waters from the Antrim shale[6,9]. The presence of ethane and propane represents the mixing of a relatively small fraction (up to 20%) of thermogenic gas with bacterial gas.

The connection among hydrology, geochemistry and gas production for the Antrim shale is not unique and will probably be applicable to other hydrogeological settings. Recent gas exploration and development in the Illinois basin targets the shallow margins of the Devonian New Albany shale, where a similar set of hydrogeological conditions exist. Non-conventional natural gas deposits, such as those in the Antrim shale, can be economic and provide ideal local energy resources because of shallow drilling depths and the geographically predictable nature of *in situ* production.

Widespread discoveries of microbial communities in the deep subsurface have led to speculation that biogenic gas may comprise a larger component of natural gas reserves than previously thought[25,26]. Non-conventional gas resources, such as coal-beds and organic-rich shales have largely been attributed to thermogenic processes[4,27], yet they may contain far more microbial gas than previously believed. Our findings should stimulate a broader view of these resources and establish integrated geochemical approaches for recognition of biogenic gas deposits. □

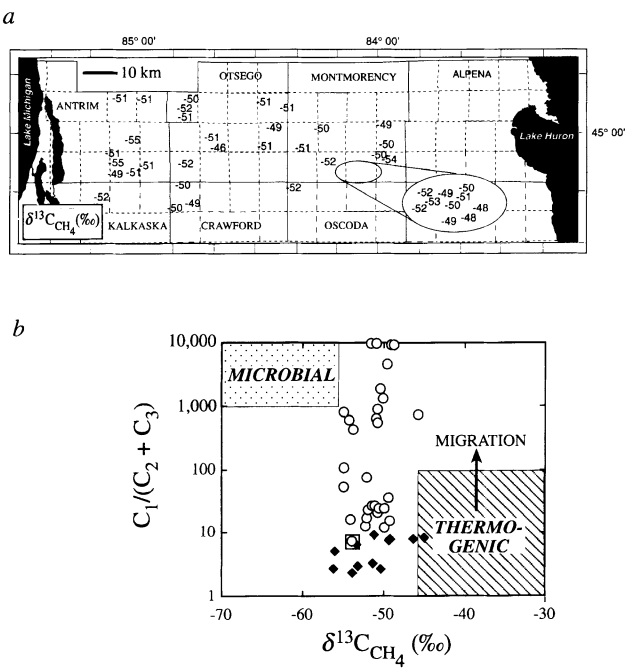

FIG. 3 *a*, $\delta^{13}C$ (w.r.t. VPDB) values for methane are plotted over well locations and are invariant across the trend. *b*, A plot of (methane/(ethane + propane)) versus $\delta^{13}C$ of methane for Antrim shale gases (open circles). Gases produced from the Silurian Niagaran limestone (filled diamonds) and Antrim shale (open square) samples from the central portion of the basin are thought to represent thermogenic gas sources[20]. Carbon isotopic composition of methane has a narrow range from −47 to −56‰ (VPDB) despite three orders of magnitude variation in log(methane/(ethane + propane)). Fields for biogenic and thermogenic gases are included (adapted from ref. 23); values for Antrim shale gas samples are located at the edge of both fields on the plot. An arrow representing expected changes in gas composition due to migration of a thermogenic gas is also displayed.

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Magnetic information affects the stellar orientation of young bird migrants

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When young birds leave on their first migration, they are guided by innate information about their direction of migration. It is generally assumed that this direction is represented twice, namely with respect to celestial rotation and with respect to the Earth's magnetic field[1,2]. The interactions between the two cue systems have been analysed by exposing hand-raised young birds during the premigratory period to cue-conflict situations, in which celestial rotation and the magnetic field provided different information. Celestial rotation altered the course with respect to the magnetic field[3–7], whereas conflicting magnetic information did not seem to affect the course with respect to the stars[8,9]. Celestial information thus seemed to dominate over magnetic information. Here we report that the interaction between the two cue systems is far more complex than this. Celestial rotation alone seems to provide only a tendency to move away from its centre (towards geographical south), which is then modified by information from the magnetic field to establish the distinctive, population-specific migratory direction.

Our experimental birds were garden warblers, *Sylvia borin*, a species of long-distance night migrants which breed in central and northern Europe and winter in tropical Africa. During migration, birds of the central European population first head southwest to Iberia, then change to a more southeasterly course to reach their African winter quarters[10]. Laboratory studies have indicated that the migratory direction of garden warblers is coded with respect to the magnetic field[11] and with respect to celestial rotation[9]. The change in direction from southwest to southeast was found to occur spontaneously at the end of September and could also be observed in the laboratory[12].

Our test birds were taken from their nests at the age of 4 to 6 days, transferred to Frankfurt am Main, and hand raised until they were self-sufficient. During the premigratory period, they were exposed to an artificial 'sky' with small lights as 'stars'[9,13], which rotated anti-clockwise with one rotation per day. Previous studies have shown that such a 'sky' could replace the natural sky in allowing stellar orientation[9] and changing the magnetic course[5]. The cage containing the birds was positioned eccentrically so that the centre of rotation coincided with magnetic north, mimicking the natural situation. The control group experienced this 'sky' together with the local geomagnetic field (47 μT, 66° inclination), whereas the experimental group experienced the sky in the absence of meaningful magnetic information, as the horizontal component of the magnetic field was compensated (90° inclination). After these exposures, which lasted from mid-July to mid-August, the birds were moved into a windowless room and housed in individual cages.

Orientation tests were done between mid-August and mid-November under the same, but now stationary, sky in a vertical magnetic field (90° inclination). This means that during testing, neither celestial rotation nor magnetic information was available; the birds had to rely entirely on the stars and what they had learned during exposure. The mean directions of both groups during the first part and the second part of the season are shown in Fig. 1; Table 1 gives the data from individual birds.

During August and September, both groups showed significant orientation, but there was a difference between their headings. The controls that had been exposed to conditions simulating the natural situation showed the seasonally appropriate tendency to orient towards the southwest, whereas the experimental group that had observed the same rotating sky without magnetic information headed southwards. This difference in mean direction was significant ($P < 0.01$, Watson–Williams test[14]). From 1 October onwards, when garden warblers normally change their course towards the southeast, no such change in direction was observed. Both continued as before ($P > 0.05$, Wilcoxon test comparing the first half and the second half of the season) with a significant increase in scatter ($P < 0.05$, Mann–Whitney test).

Our findings indicate that the magnetic field is crucial for the development of the population-specific migratory direction with respect to the stars. Garden warblers must observe the rotating sky together with magnetic information during the premigratory period to establish, with respect to the stars, the specific south-

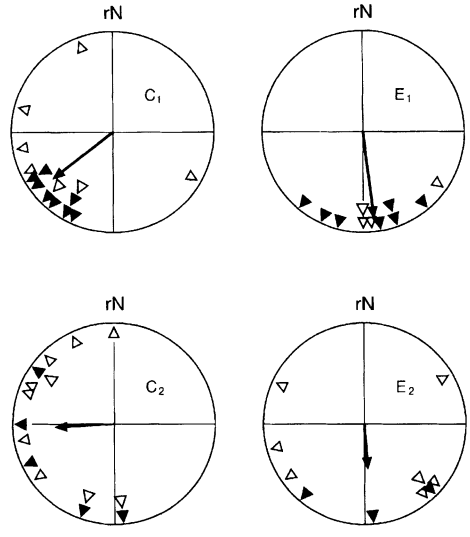

FIG. 1 Orientation of young garden warblers under a stationary artificial sky in the absence of meaningful magnetic information. Left, controls (C) that had been exposed, during the premigratory period, to the same, but rotating, sky in the geomagnetic field; right, experimental (E) birds that had been exposed to the same rotating sky in the absence of magnetic information. Top, August and September; bottom, October and November. The triangles indicate the mean directions of individual birds (filled, significant; open, not significant); the arrows represent the second-order mean vectors based on these directions proportional to the radius of the circle. rN, rotational north.
METHODS. The birds were tested in octagonal cages (1 m diameter, 35 cm high) with eight radially positioned double perches[19]. Their activity was recorded by switches connected to the perches. From the distribution of the activity, the heading of each individual test night was calculated by vector addition. A mean vector was calculated from the headings of each individual bird. The data were analysed using standard procedures of circular statistics[14].