Termite mounds harness diurnal temperature oscillations for ventilation

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Many species of millimetric fungus-harvesting termites collectively build uninhabited, massive mound structures enclosing a network of broad tunnels that protrude from the ground meters above their subterranean nests. It is widely accepted that the purpose of these mounds is to give the colony a controlled microclimate in which to raise fungus and brood by managing heat, humidity, and respiratory gas exchange. Although different hypotheses such as steady and fluctuating external wind and internal metabolic heating have been proposed for ventilating the mound, the absence of direct in situ measurement of internal air flows has precluded a definitive mechanism for this critical physiological function. By measuring diurnal variations in flow through the surface conduits of the mounds of the species *Odontotermes obesus*, we show that a simple combination of geometry, heterogeneous thermal mass, and porosity allows the mounds to use diurnal ambient temperature oscillations for ventilation. In particular, the thin outer flutelike conduits heat up rapidly during the day relative to the deeper chimneys, pushing air up the flutes and down the chimney in a closed convection cell, with the converse situation at night. These cyclic flows in the mound flush out CO_2 from the nest and ventilate the colony, in an unusual example of deriving useful work from thermal oscillations.

termite mound | ecosystem engineering | ventilation | niche construction | thermodynamics

Many social insects that live in dense colonies (1, 2) face the problem of keeping temperature, respiratory gas, and moisture levels within tolerable ranges. They solve this problem by using naturally available structures or building their own nests, mounds, or bivouacs (3). A particularly impressive example of insect architecture is found in fungus-cultivating termites of the subfamily Macrotermitinae, individually only a few millimeters in body length, which are well known for their ability to build massive, complex structures (4, 5) without central decision-making authority (6). The resulting structure includes a subterranean nest containing brood and symbiotic fungus, and a mound extending $\sim$ 1–2 m above ground, which is primarily entered for construction and repair, but otherwise relatively uninhabited. The mound contains conduits that are many times larger than a termite (5), and viewed widely as a means to ventilate the nest (7). However, the mechanism by which it works continues to be debated (8–11).

Ventilation necessarily involves two steps: transport of gas from underground metabolic sources to the mound surface, and transfer of gas across the porous exterior walls with the environment. Although diffusion can equilibrate gradients across the mound surface (12), it does not suffice to transport gas between nest and surface. (It takes gas $\sim$ 4 d to diffuse 2 m.) Thus, ventilation must rely on bulk flow inside the mound. Previous studies of mound-building termites have suggested either thermal buoyancy or external wind as possible drivers, making a further distinction between steady [e.g., metabolic driving (11), steady wind] and transient [e.g., diurnal driving (9, 10), turbulent wind (8)] sources. However, the technical difficulties of direct in situ measurements of airflow in an intact mound and its correlation with internal and external environmental conditions have precluded differentiating between any of these

hypotheses. Here, we use both structural and dynamic measurements to resolve this question by focusing on the mounds of *O. obesus* (Termitidae, Macrotermitinae), which is common in southern Asia in a variety of habitats (13).

In Fig. 1*A*, we show the external geometry of a typical *O. obesus* mound, with its characteristic buttresslike structures (flutes) that extend radially from the center (Fig. 1*B*). The internal structure of the mound can be visualized using by either making a horizontal cut (Fig. 1*C*) or endocasting (Fig. 1*D*). Both approaches show the basic design motif of a large central chimney with many surface conduits in the flutes; all conduits are larger than termites, most are vertically oriented, and well connected. (A simple proof of well connectedness is that gypsum injected from a single point can fill all interior conduits.) This macroporous structure can admit bulk internal flow and thus could serve as an external lung for the symbiotic termite–fungus colony.

To understand how the mound interacts with the environment, we first note that the walls are made of densely deposited granules of clay soil, forming a material with high porosity (37–47% air, by volume; *SI Appendix*), and small average pore diameter ($\sim$ 5 μm, roughly the mean particle size). Indeed, healthy mounds have no visible holes to the exterior, and repairs are quickly made if the surface is breached. The high porosity means that the mound walls provide little resistance to diffusive transport of gases along concentration gradients. However, the small pore size makes the mound very resistant to pressure-driven bulk flow across its thickness. Thus, the mound surface behaves like a breathable windbreaker. Finally, the low wind speeds observed around the termite mounds of $\sim 0 - 5$ m/s implies that they are not capable of creating

Fig. 1. Mounds of *O. obesus*. Viewed from (*A*) the side, (*B*) top, and by (*C*) cross-section. Filling the mound with gypsum, letting it set, and washing away the original material reveals the interior volume (white regions) as a continuous network of conduits, shown in *D*. Endocast of characteristic vertical conduit in which flow measurements were performed, near ground level, toward the end of flutes, indicated by the arrow (*E*).

significant bulk flow across the wall, effectively ruling out wind as the primary driving source.

Within the mound, a range of indirect measurements of CO_2 concentration, local temperature, condensation, and tracer gas pulse chase (8–10, 11, 14) show the presence of transport and mixing. However, a complete understanding of the driving mechanism behind these processes requires direct measurements of flow inside the mound. This is difficult for several reasons. First, the mound is opaque, so that any instrument must be at least partly intrusive. Second, expected flows are small ($\approx$centimeters per second), outside the operating range of commercial sensors, requiring a custom-engineered device. Third, because conduits are vertical, devices relying on heat dissipation, or larger, high heat capacity setups can generate their own buoyancy-driven (and geometry dependent) flows, making measurements ambiguous (15). Finally, and most importantly, the mound environment is hostile and dynamic. Termites tend to attack and deposit sticky construction material on any foreign object, often within 10 min of entry. If one inserts a sensor even briefly, termites continue construction for hours, effectively changing the geometry and hence the flow in the vicinity of the sensor.

To measure airflow directly, we designed and built a directional flow sensor composed of three linearly arranged glass bead thermistors, exposed to the air (*SI Appendix*). A brief pulse of current through the center bead creates a tiny bolus of warm air, which diffuses outward and is measured in either neighboring bead. (The operating mechanism is similar in principle to that of ref. 16.) Directional flow along the axis of the beads biases this diffusion, and is quantified by the ratio of the maximum response on each bead, measured as a temperature-dependent resistance. In a roughly conduit-sized vertical tube, this resistance–change metric depends linearly on flow velocity, with a slight upward bias due to thermal buoyancy. This allows us to measure both flow speed and direction locally. The symmetry of the probe allows for independent calibration and measurement in two orientations by rotating by 180° (arbitrarily labeled upward and downward; *SI Appendix*).

In live mounds, the sensor was placed in a surface conduit at the base of a flute for $\lesssim$ 5 min at a time to avoid termite attacks, which damage the sensors. For a self-check, the sensor was rotated in place, such that a given reading could be compared on both upward and downward calibration curves. We also measured the flow inside an abandoned (dead), unweathered mound that provided an opportunity for long-term monitoring without having termites damage the sensors. Simultaneous complementary measurements of temperature in flutes and the center were taken. To measure the concentrations of CO_2, a metabolic product, a tube was inserted into the nest; in one mound in the center slightly below ground and another in the chimney at $\approx$ 1.5 m above. Gas concentration measurements were made every 15 min by drawing a small volume of air through an optical sensor from the two locations for most of one uninterrupted 24-h cycle.

Nearly all of the 25 mounds that were instrumented were in a forest with little direct sunlight. In Fig. 2*A*, we show flow measurements in 78 individual flutes of these mounds as a function of time of day. We see a clear trend of slight upward (positive) flow in the flutes during the day, and significant downward (negative) flow at night. The data saturates for many night values, as the flow speed was larger than our range of reliable calibration (*SI Appendix*). In Fig. 2*B*, we show the flow rate for a sample flute in the abandoned mound. Notably, it follows the same trend seen in live mounds, but the flow speeds at night are not nearly as large as for the live mounds. For both live and dead mounds, we also show the
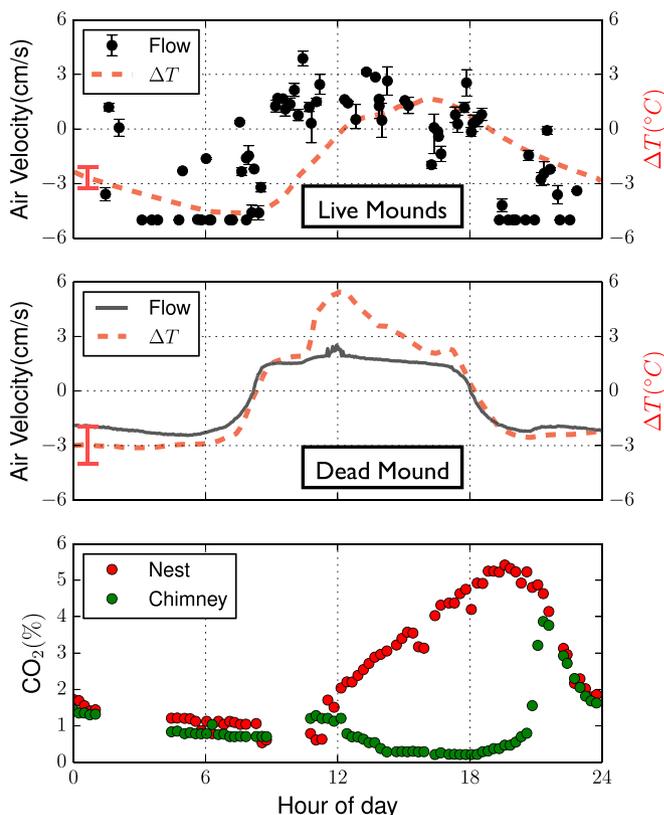
Fig. 2. Diurnal temperature and flow profiles show diurnal oscillations. (*Top*) Scatterplot of air velocity in individual flutes of 25 different live mounds (•). Error bars represent deviation between upward and downward $\approx$ 1.5-min flow measurements. The dashed red line is the average difference between temperatures measured in four flutes and the center (at a similar height), ΔT, in a sample live mound (Representative error bar shown at left). (*Middle*) Corresponding flow and ΔT, continuously measured in the abandoned mound. (*Bottom*) CO_2 schedule in the nest (•) and the chimney 1.5 m above (•), measured over one cycle in a live mound (Movie S1).

Fig. 3. (*Top*) Thermal images of the mound in Fig. 1*A*, during the day and night qualitatively show an inversion of the difference between flute and nook surface temperature. Bases of flutes are marked with ovals to guide the eye. (*Middle* and *Bottom*) Mechanism of convective flow illustrated by schematic of the inverting modes of ventilation in a simplified geometry. Vertical conduits in each of the flutes are connected at top and in the subterranean nest to the vertical chimney complex. This connectivity allows for alternating convective flows driven by the inverting thermal gradient between the massive, thermally damped, center and the exposed, slender flutes, which quickly heat during the day, and cool during the night.

difference in temperature measured between the flutes and center, $\Delta T = T_{flute} - T_{center}$, and see that it varies in a manner consistent with the respective flow pattern. This rules out metabolic heating (11) as a central mechanism, because a dead mound shows the same gradients and flows as a live one.

In Fig. 2*C* we show that the accumulation of respiratory gases also follows a diurnal cycle, with two functioning states (Movie S1). During the day, when flows are relatively small, CO_2 gradually builds up to nearly 6% in the nest, and drops to a fraction of 1% in the chimney. At night, when convective flows are large, CO_2 levels remain relatively low everywhere. Although it is surprising that these termites allow for such large periodic accumulations of CO_2, similar tolerance has been observed in ant colonies (17).

In addition to measuring these slowly varying flows, we used our flow sensors in a different operating mode to also measure short-lived transient flows similar to those of earlier reports (8, 15). This requires a different heating protocol, wherein the center bead is constantly heated, so that small fluctuations in flow lead to antisymmetric responses from the outer beads. However, the steady heating leads to a trade-off, as thermally induced buoyancy hinders our ability to interpret absolute flow rate. Our measurements found that transients are at most only a small fraction (≈millimeters per second) of average flow speeds under normal conditions, and were not induced by applying steady or pulsing wind from a powerful fan just outside the termite mound. Pulse chase experiments on these mounds, in which combustible tracer gas is released in one location in the mound and measured in another, gave an estimate of gas transport speed (not necessarily the same as flow speed) of the same order (≈centimeters per second), which indicates that our internally measured average flow is the dominant means of gas transport and mixing with no real role for wind-induced flows. Furthermore, temperature measurements in the center at different heights showed that the nest is almost always the coolest part of the mound central axis, additional evidence against the importance metabolic heating (11) (*SI Appendix*).

Taken together, these results point strongly to the idea that diurnally driven thermal gradients drive air within the mound,

facilitating transport of respiratory gases. Observations of the well connectedness of the mound and the impermeability of the external walls imply that flow in the center of the mound, to obey continuity, must move in the vertical direction opposite that of the flutes. When the flutes are warmer than the interior, air flows up in the flutes, pushing down cooler air in the chimney. The opposite occurs when the gradient is reversed at night (Fig. 3). (The air flowing down the flutes is significantly warmer than ambient temperature, a situation only possible if it were being pushed by even warmer air flowing up the chimney.)

This model predicts flow speeds comparable to those observed in the mound (*SI Appendix*), and is consistent with the quick uptake and gradual decline of CO_2 measured in the chimney; with the evening temperature inversion, convection begins to push rich nest air up the chimney before diffusion across the surface gradually releases CO_2 from the increasingly mixed mound air. (See Movie S1 for a sequence of thermal images of the inversion that accompanies this drop.) This forcing mechanism is inherently transient; if the system ever came to equilibrium and the gradient disappeared, ventilation would stop.

It has long been thought that animal-built structures, spectacularly exemplified by termite mounds, maintain homeostatic microhabitats that allow for exchange of matter and energy with the external environment and buffer against strong external fluctuations. Our study quantifies this by showing how a collectively built termite mound harnesses natural temperature oscillations to facilitate collective respiration. The radiatorlike architecture of the structure facilitates a large thermal gradient between the insulated chimney and exposed flutes. The mound harnesses this gradient by creating a closed flow circuit that straddles it, promoting circulation, and flushing the nest of CO_2. Although our data comes entirely from one termite species, the transport mechanism described here is very generic and is likely dominant in similarly massive mounds with no exterior holes that are found around the globe in a range of climates. A natural question that our study raises is that of the rules that lead to decentralized construction of a reliably functioning mound. Although the insect behavior that leads to construction of these mounds is not well understood, it is likely that feedback cues are important. The knowledge of the internal airflows and transport mechanisms might allow us to get a window into these feedbacks and thus serve as a step toward understanding mound morphogenesis and collective decision making.

The swarm-built structure described here demonstrates how work can be derived, through architecture, from the fluctuations of an intensive environmental parameter—a qualitatively different strategy than that of most human engineering that typically (18) extracts work from unidirectional flow of heat or matter. Perhaps this might serve to inspire the design of similarly passive, sustainable human architecture (19, 20).

Experimental Procedures

Steady Flow Measurement. In an area within walking distance of the campus of National Centre for Biological Sciences Bangalore, India, 25 mounds were chosen that appeared sufficiently developed (≳ 1 m tall) and intact. All mounds were located in at least partial shade, but received direct sunlight intermittently during the day. [Direct sunlight does not appear to play a direct role in the flow schedule (*SI Appendix*). Full exposure would lead to orientational dependence of temperature and air flows.] The scatter plot of steady flow (Fig. 2*A*) represents individual measurements of the flow in the large conduits found at the end of each available flute.

To place the probe, a hole was manually cut with a hole saw fixed to a steel rod, usually to a depth of about 1–3 cm before breaking into the conduit. With a finger, the appropriate positioning and orientation of the sensor was determined. Occasionally, the cavity was considered too narrow (≲ 3 cm diameter), or the hole entered with an inappropriate angle, in which case it was sealed with putty and another attempt was made.

Because internal reconstruction, involving many termites and wet mud, continues long after any hole is made, the same flute was never measured

twice. In a round of measurements, flows in 1–3 (out of approximately 7 available) flutes of each of ∼ 8 nearby mounds were measured, a process which took several hours. Each of the 25 mounds was visited 2–3 times to use unmeasured flutes, but deliberately at different times of day to avoid possible correlations between mound location and flow pattern.
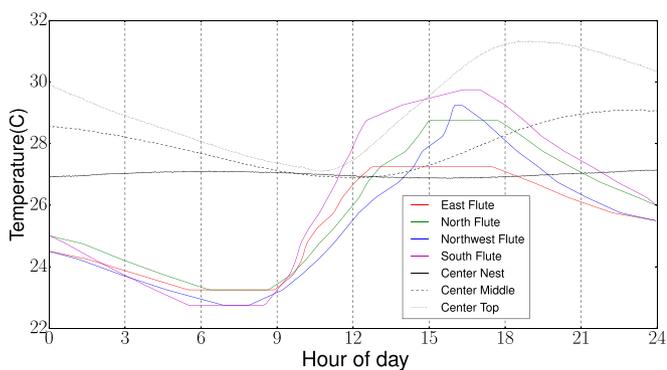
An individual measurement of flow was taken for ∼ 2 min in each orientation, such that the response curves from which the metric and then flow are calculated are averaged over many pulses (∼ 6 pulses per min). The error bar of each constant flow velocity measurement in Fig. 2A indicates the deviation in measured flow between orientations. Care was taken to ensure that the probe temperature remained close to the interior flute temperature, and no long-term drift in measured velocity was observed as the probe equilibrated. Periodically between measurements, the sensor was tested in the same apparatus to check that it remained calibrated, especially when thermistors were damaged or dirtied by termites and needed to be cleaned.

The dead mound referenced in the text was identified as such because no repairs were made upon cutting holes for the sensor. As it was also intact (there were no signs that erosion had yet exposed any of the interior cavities) and within reach of electricity, it was possible to make continuous flow measurements that could be compared with the brief measurements for live mounds.

Geometry and Sources of Error in Flow Measurement. In situ measurements take place in a complex geometry, and the width, shape, and surrounding features can be highly variable. This can lead to significant variation in local velocities, even causing some local velocities to go against the average trend; this is a generic feature of flow through disordered, porous media (21, 22). In addition, the width, shape, and impedance of a channel are different from in our calibration setup, and the position of the probe within a channel could not be exactly known. These factors are most likely the dominant source of error for any given measurement in the field, either over- or underestimating the flow in a particular conduit. This error, though potentially as large as a factor of ∼ 2, is reflective of the natural variation in mound geometry, is not correlated to any other parameter, and cannot mistake the direction of flow, such that the trend in average flow remains unambiguous.

Temperature Measurements. Temperatures in the dead mound reported in Fig. 2B in the main text were obtained by implanting iButtons (DS1921G; Maxim) into the mound using the hole saw and closing the openings with wet mud. Two iButtons were placed in flutes at the same location where flow data had been acquired. Another two iButtons were placed 5–10 cm below the surface, in the nooks between flutes, such that they were located roughly in the periphery of the central chimney. As shown in Fig. 2, ΔT was calculated as the temperature from the measured flute minus the average temperature measured by the centrally placed iButtons. The raw data were slightly smoothed before taking the difference, to reduce distracting jumps in data from the iButtons, which have a thermal resolution of 0.5 C.

In the large healthy mound, digital temperature/humidity sensors (SHT11; Sensiron) were implanted at different heights near the central axis. Screened windows protected the sensors from direct contact by termites and building material, and remain coupled to the interior environment. The sensors and Arduino were powered with a high capacity 12-V lead acid battery and they
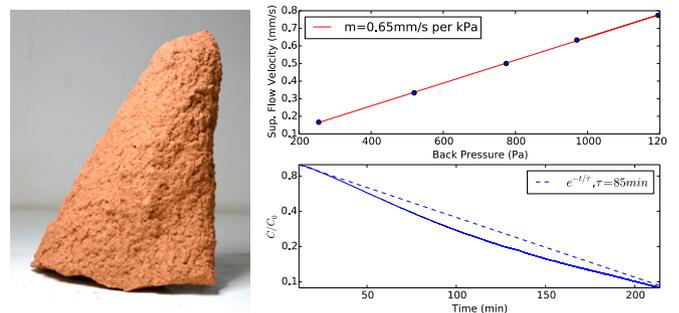
recorded temperature for approximately two days. The iButtons were placed in the bases of flutes in four sides of the same mound. Temperature differences reported in Fig. 2A were calculated from the average of flute temperatures and central axis temperature at the corresponding height.

Moreover, there is not much of a dependence of the temperature along the center of the mound on cardinal direction, as seen in Fig. 4, consistent with the fact that these mounds are not directly heated by the sun. Finally, we note that the temperature differences between interior and flutes shown in Fig. 1 are significantly larger at night than during the day. This and/or the vertical asymmetry of the convective cell (in that the flutes are closer to the top of the convective cell) might be responsible for the observed asymmetry in flow magnitudes between night and day.

Permeability and Diffusibility. A hollow, conical sample of a flute was cut from a mound. The bottom was sealed with gypsum, such that the pores in the wall material and length of plastic tubing are the only path in and out of the cone. Air was pulled by a vacuum pump from the tube through the volumetric flow meter. The pressure differential between inside and outside of the cone was measured by the displacement of water in a column between the cone and flow meter. Fig. 5, *Left* shows the 20-cm-tall conical sample and *Right Top* relationship between back pressure and average flow. From this graph, one can read the local flow induced across the mound wall due to a pressure differential from incident wind. Wind in the area during the study was typically in the range 0–5 m/s, which could produce a maximum dynamic pressure $P = \frac{1}{2}\rho v^2 = 0$–15 Pa, giving a maximum flow through the surface of 0.01 mm/s. With even the most liberal approximations, this is not enough to produce bulk flow of the order we measured, in agreement with the observed negligibly small transient flows in tests with a powerful fan. If macroscopic holes penetrated the mound surface in some locations, they would dramatically change the permeability estimate of the mound as a whole. However, such holes were not observed in these mounds, and the species seems to fill in even the smallest holes. This behavior contrasts that of other species, which appear to tolerate some holes; *O. obesus* actively closed narrow holes made for the CO_2 measurement, and we have observed that *Macrotermes michaelseni* in Namibia did not.

Impermeability to bulk flow of the wall does not mean nonporous or impermeable to diffusion. Cooking gas was injected into the conical sample and measured by combustible gas sensor that was sealed inside the conical sample. Fig. 5, *Right Bottom* shows that it diffuses out the surface over the course of about 2 h (following close to exponential decay).

CO_2 Measurements. One large (∼2 m tall), apparently healthy mound was chosen (that shown in Figs. 1 *A* and *B* and 3; Movie S1) for measurements. One hole was drilled from ground level diagonally down into the nest and another into the central chimney 1.5 m above ground. Then 1/4 inch tubing was inserted in the holes and left overnight such that the termites sealed the holes at the surface leaving the tubes snugly in place. A Cozir wide range IR LED CO_2 sensor was fitted with a custom machined, air-tight cap with two nozzles, such that air pulled into the cap would gradually diffuse across the sensor membrane and the response could be recorded with an Arduino onto a laptop computer. For most of one 24-h cycle, every 15 min air was drawn from each of the tubes in the mound through the sensor with a 50-mL syringe, pulling gradually until the response leveled out, meaning the full concentration of mound air had diffused across the sensor membrane. When termites periodically sealed the end of the tube inside the mound, a few milliliters of water was forced into the tube, softening and breaking the seal so measurements could continue.

Fig. 4. Temperatures along the center of healthy, ∼ 2 m tall, mound at three heights: "nest" (∼ 30 cm below ground), "middle" (∼ 50 cm above ground), and "top" (∼ 130 cm above ground), and in bases of flutes at four cardinal directions. Error in values along the center is (±0.4° C), and (±1° C) in the flutes. The independence of behavior on cardinal direction shows direct solar heating is not of primary importance.

Fig. 5. (*Left*) A hollow conical sample from a mound flute. (*Right*) Flow velocity as a function of back pressure measured by sealing the bottom and pulling air into the sample (*Top*), and loss of combustible gas by diffusion in same sample (*Bottom*).

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Prediction of Mean Flow Speed. As a model for a convective circuit within a termite mound, we choose a pipe radius r, in the shape of a closed vertical loop of height h, where the temperature difference between left and right side of the loop is ΔT. The total driving pressure is $\rho\alpha\Delta Tgh$, where ρ is air density and α is the coefficient of thermal expansion, and Poiseuille's law gives

$$Q = \underbrace{\rho\alpha\Delta Tgh}_{\text{Driving Pressure}} \cdot \underbrace{\frac{\pi r^4}{8\mu h \cdot 2}}_{\text{Poiseuille Resistance}}, \qquad [1]$$

where the factor of 2 comes from the resistance on both sides of the loop. Calculating flow speed:

$$V = \frac{Q}{\pi r^2} = \frac{\rho\alpha\Delta Tgr^2}{16\mu}, \qquad [2]$$

and plugging in values of $\Delta T = 3°C$, $r = 3$ cm, $\mu/\rho = 0.16$ cm^2/s, and $\alpha = \frac{1}{300°C}$, we obtain a result of ~ 35 cm/s. This speed is ~ 10 times higher than those observed, likely due to oversimplifying internal geometry; disorder and variation in conduit size favors high-resistance bottlenecks that reduce the mean flow speed. The calculation demonstrates that observed thermal gradients and crude dimensions are sufficient to produce flow of the order measured.

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