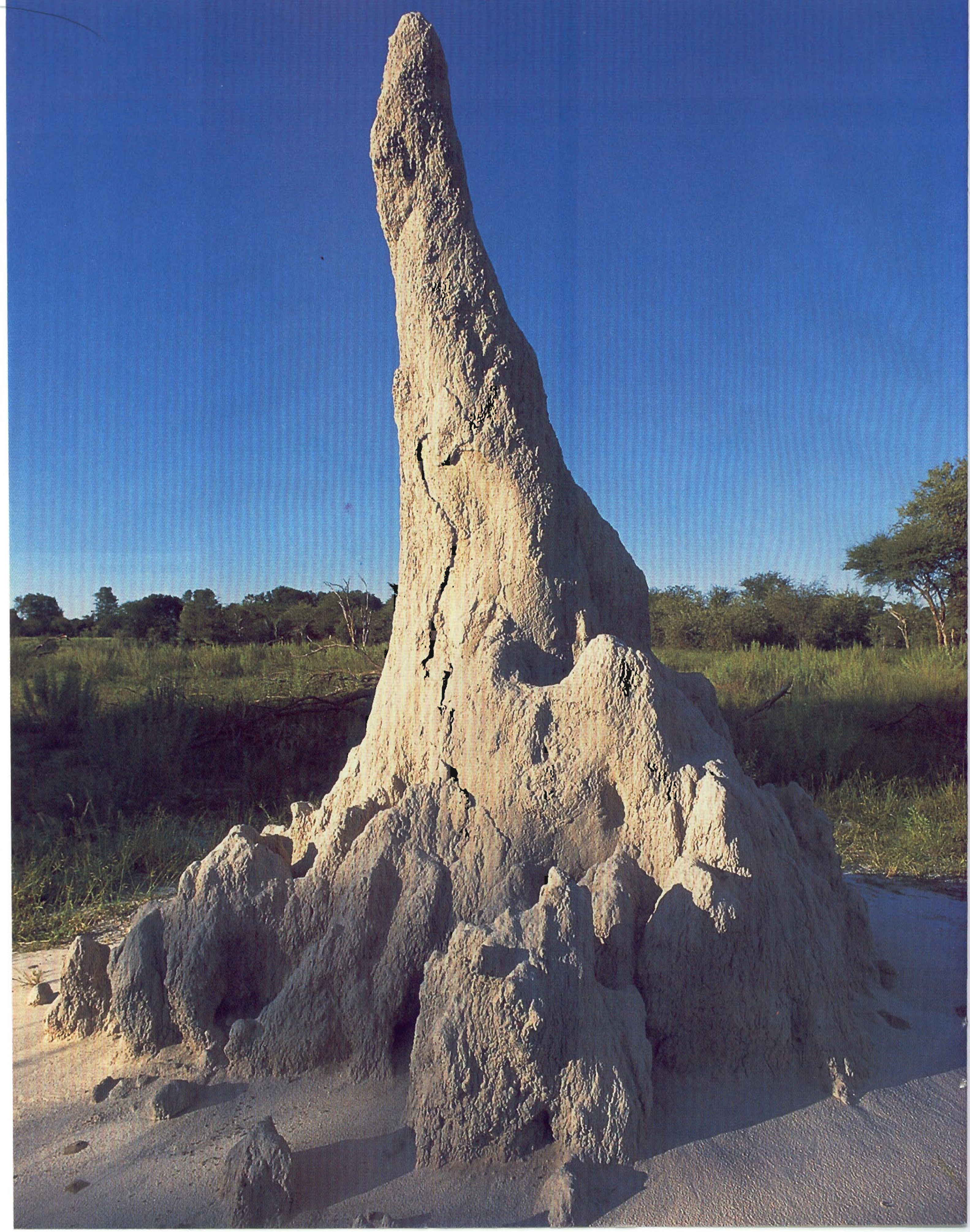

A Superorganism's Fuzzy Boundaries

The breathing termite mounds of southern Africa raise the question, Where does "animate" end and "inanimate" begin?

By J. Scott Turner

They look like the curlicue-topped mountain that overlooks the Grinch's Whoville: cones of soil and sand, up to thirty feet tall, topped with earthen spires pointing toward the noon sun. Common on the savannas of southern Africa, they are termite mounds, constructed by the fungus-cultivating termite *Macrotermes michaelseni*. Locals call these structures "ant heaps." In Afrikaans, termites are *rysmeere* (literally, rice ants); sometimes the insects are called white ants. Termites are not ants, however: their ancestors are social cockroaches, not the wasps from which ants descend. And neither is the termite mound a heap, a haphazard pile of dirt. Opening it reveals a complicated internal architecture: a capacious central chimney from which radiates a complex network of passages, connecting ultimately to an array of thin-walled tunnels that lie under the mound's surface like veins on an arm. Most interesting, though, is what you do not see: termites. The mound is not a habitation for the millions of termites that built it. Their residence is a nest below the mound, a spherical underground city about six feet in diameter.

The mound's internal architecture betokens its purpose. The mound ventilates the nest, a service that the termites desperately need. A few tiny termites may not breathe much, but a couple million of them together consume oxygen at a rate roughly that of a large rabbit. And the termites are not the only heavy breathers in the nest.

Macrotermes species each grow a particular species of fungus that predigests the termites' food. The insects swallow grass, bark, dead wood, and undigested matter in other animals' fecal pellets and quickly pass them, undigested, within the nest, where the fungus can break down the material. This fungus, together with bacteria and other soil microorganisms, raises the oxygen requirement to the amount needed by a cow. Indeed, ranchers in northern Namibia think of each termite mound as the equivalent of one livestock unit: each nest's foraging insects eat about the same quantity of grass as would one head of cattle. A cow buried alive would soon die without access to air, and so it is with a termite colony: without ventilation, it would suffocate.

PAUL FRANKLIN; OXFORD SCIENTIFIC FILMS

Entomologists have long ascribed respiratory functions to these termite mounds, and for many years they thought the mound's workings were pretty well understood. It was a fine story, first told in the late 1950s by Swiss scientist Martin Lüscher, who was investigating the mounds of *Macrotermes natalensis*. Lüscher had the ingenious, but at best only partly correct, idea that a colony's metabolism could power its ventilation and maintain the nest's remarkably constant temperature. The energy of the termites' collective "hot breath" heated the air in the nest, Lüscher surmised, and the warmed air would waft up through the mound's tunnels. The air rising from the nest would eventually cool and pass down again through the conduits near the mound's surface. In these passages, the air would be refreshed by diffusion through the structure's porous walls before being sent on another circuit through the nest.

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Opposite page: A huge mound built by a colony of *Macrotermes* termites ventilates a subterranean nest. Mounds can reach a height of thirty feet. Workers, above, take about a year to put together a mound.

Lüscher's scheme (a version of what is known as thermosiphon ventilation) seemed to provide a model for the environmental regulation of termite colonies. This sort of self-regulating process is known as homeostasis. The human body's maintenance of a certain internal temperature is an ex-

ANTHONY BANNISTER; NHPA

A tiny, pale *Macrotermes* worker and a much larger soldier rely on the fungus *Termitomyces* (the white balls) for help in digesting cellulose.

ample. In *social* homeostasis, members of a colony coordinate their behavior to regulate their environment. Bees, for instance, collectively regulate hive temperature. When the weather is cold, they cluster into compact balls and shiver, warming the hive. When the weather turns hot, workers fan their wings at the entrance to the hive, cooling it. Hive temperature thus remains steady despite changes on the outside. Thermosiphon ventilation supposedly provided a termite colony with the capacity for achieving homeostasis. Together the insects built a mound: this constituted the social aspect. And when, for example, the colony generated more heat than it dissipated, accumulated heat would warm the nest air, making it more buoyant and moving it more rapidly through the structure. The accelerated ventilation would then cool the colony back down.

As beautiful as Lüscher's idea was, though, it never quite added up. For one thing, thermosiphon ventilation requires that the mound have a rather specific architecture. How could the termites collectively "know" how to build the mound properly, and if they didn't get it right, how would they "know" it was wrong or how to fix it? Other things, too, simply didn't fit. Lüscher thought of the mounds as air conditioners. But the temperature in underground chambers is inherently steady, so a mound built to cool a subterranean nest seems superfluous. Experiments in which termite mounds were capped put the lid on the air-conditioning hypothesis, because the temperature in the nests did not change.

But if the mound isn't an air conditioner, what is it? The problem captivated me. I thought that the mound had to do something besides passively connect the nest to the air outside, if only because building such a structure is an enormous investment of energy and time: a *Macrotermes* mound contains, on average, about five cubic yards of soil and takes a mature colony about one year to build. Perhaps the mound controlled—if not nest temperature—some other aspect of the nest environment, such as humidity or concentrations of oxygen or carbon dioxide. Aided by a grant from the Earthwatch Institute, I went off to Namibia to look into the matter.

I had one big advantage that Martin Lüscher did not: miniature sensors that allowed me not only to measure in great detail the composition of the nest atmosphere but also to trace precisely how air moved through the tunnels of the nest and mound. The results were, shall we say, mixed. I was gratified to find that levels of oxygen and humidity in the nest were steady—and also different from the external world—as I thought they would be. Oxygen concentration averaged about 19 percent, compared with 21 percent in the atmosphere, and the humidity was 70 percent inside, compared with about 20 percent outside. But the movements of air I observed were puzzling. Not only was Lüscher's metabolism-driven circulation absent; the air seemed to move with no pattern at all.

But after three years of tracing flows in mounds and nests, taking apart several mounds to work out their architecture, and doing a lot of head scratching, I finally came to a pretty good understanding of how a mound operates. Metabolism does not power ventilation, as Lüscher thought. The wind does. By building the mound upward into the stiffer breezes higher off the ground, the termites harness the wind to drive air movements in the mound's tunnels. The flow of the wind pushes air through the porous soil on the windward side and sucks it out on the leeward side, allowing the nest atmosphere to mix with fresh air from the outside world. This in itself is not surprising; lots of animals build structures that do similar things. What is remarkable is the pattern of ventilation: an in-and-out movement very similar to the way air flows into and out of our own lungs. In fact, what most distinguishes the action of the two "organs" is that the termites' is powered by the ebb and flow of wind instead of by the contractions of muscle.

I also got a pretty good idea of how the mound fits into the socially homeostatic system that regulates the nest's atmosphere. Understanding the system requires thinking about the mound as not really an object but a process. Each year, the workers incorporate about a cubic yard of soil into the mound; meanwhile, the mound is eroding at about the same rate. Its structure is therefore a continually shifting balance between the locations on the mound where soil is added or removed and the rate at which the soil movement occurs. I learned that termites build or excavate the mound in reaction to the atmosphere inside the nest, making the mound a "smart" structure. If the nest is too stuffy, for example, the insects increase the upward rate of soil movement, extending the mound higher, into stiffer winds and more energetic ventilation. Linking soil transport with nest atmosphere results in homeostasis as the mound's structure is continually adjusted and readjusted to meet the "Goldilocks criterion": capturing wind that's not too strong and not too weak but ju-u-u-u-st right.

Macrotermes *termites cultivate a particular species of fungus that predigests their food.*

A puzzling question remains, however. The fungi are the major heavy breathers in the nest, consuming oxygen about five times faster than the termites do. Why, then, do the termites work so hard to build an earthen lung if the fungi, *Termitomyces,* actually do the most to make the nest air stuffy? To be sure, the act is not altruistic, because the fungi, by breaking down the termites' food, are performing a critical function. In a sense, the termites are "paid" for their work. But the fungi may be gaining much more than simply having termites supply them with a steady diet of cellulose: *Termitomyces,* you see, have competitors.

The nest is an ample resource for any fungus that can digest cellulose, and some, such as the common wood-rotting fungus *Xylaria,* consume so much so quickly that they are not very good at sharing this resource—either with other fungi or with termites. Via their feces, the termites inadvertently introduce into the mound the spores of many of these potential competitors. If the competitors were allowed to grow, they would quickly overwhelm the slower-growing *Termitomyces,* leaving both fungus and termite in the lurch. Yet only *Termitomyces* spores germinate and grow in the nest: the growth of all other fungi is suppressed, most likely by carbon dioxide, which exists at higher concentrations within the nest than in the normal atmosphere. *Macrotermes* do not build mounds to favor *Termitomyces*

Below: *Termitomyces* fungi push through the mound to produce mushrooms at the surface. Below left: Within the mound, they also flourish in "fungus combs" built for them by the termites.


MARK COLLINS: OXFORD SCIENTIFIC FILMS


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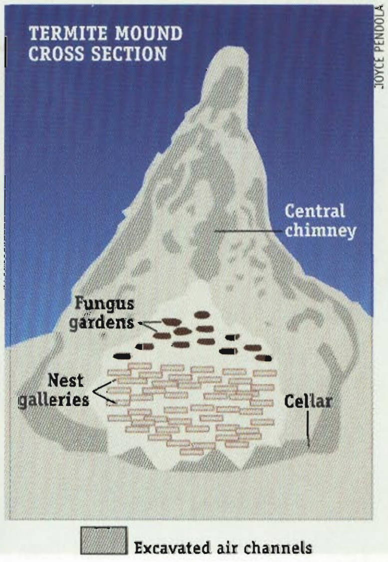
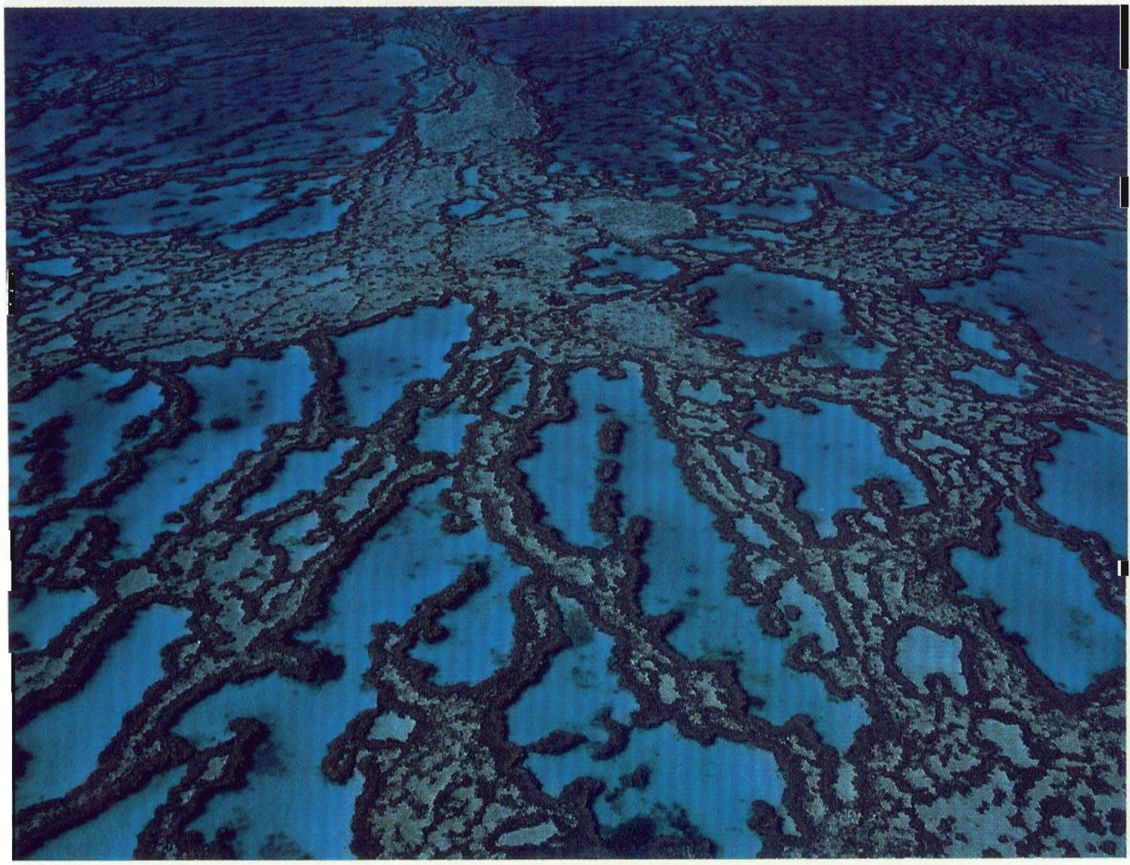


JOYCE PENDOLA

over other fungi just because the insects have some peculiar affinity for them. Rather, *Termitomyces* may be manipulating the building behavior of its termite hosts to provide an environment that suppresses the growth of the greedy species of fungi. In this sense, it may be the fungus that has cultivated the termites rather than the other way round.

The origin of such cooperation has been a puzzle for Darwinism ever since, well, Darwin. Putting energy into achieving homeostasis must provide genetic payoffs for those investing in it, or the behavior will disappear. Within an individual multicellular organism, balancing the activities of all the cells ultimately promotes the survival of only a few—the sperm or the eggs. However, since each of these gametes contains half the genetic material found in the cells that support it, there's still a payoff for all these nonreproducing support cells. A similar logic explains social homeostasis in social insects, whose "gametes"—the breeding caste—are genetically very similar to the sterile workers. But in genetically disparate groups, such as the coalition between *Macrotermes* and *Termitomyces*, some participants may not necessarily compensate others for investments in their reproductive success. Yet the termite colony is nothing if not a melding of disparate genetic interests. This melding, however, derives from common and interacting *physiological* interests and is directed at maintaining a particular association *(Macrotermes–Termitomyces)* while cutting out the possibility of other associations (such as *Macrotermes–Xylaria*). Thus the regulated environment, maintained by a constructed physiological organ—the mound—furthers the interests of both groups of inhabitants. The termite colony—insects, fungus, mound, and nest—becomes like any other body that is composed of functionally different parts working in concert and is ultimately capable of reproducing itself. Taken as a whole, the colony is an extended organism.

NURIDSANY AND PERENNOU; PHOTO RESEARCHERS, INC.



JEAN-PAUL FERRERO; AUSCAPE

Extended physiology: The spider *Argyroneta aquatica*, right, builds an external gill by weaving an underwater web and filling it with air, allowing for the exchange of respiratory gases. Below: Coral reefs, like termite mounds, are the products of the joint evolution of the animate and the inanimate.

Organisms whose physiology extends well outside their bodies are in fact quite common in nature. These lifeforms pose interesting paradoxes. For example, which parts of an extended organism are alive and which are not? In the case of termite mounds, the termites and fungi certainly qualify as living, but so does the mound, in a sense. After all, it does just what our lungs do for us. The primary difference is in perspective. For a human, what is inside the body is pretty clear, but for the termite colony, "inside" includes the nest environment. And if the physiology of the colony extends beyond the organisms the group comprises, could extended organisms and the structures they build be directed toward the physiological regulation of ecosystems—or of Earth itself?

Those scenarios may seem unlikely, but the influence of extended physiology can be enormous, producing ecosystem-wide effects, even though the power of any given external physiological adaptation (such as aquatic beetles or water spiders using bubbles as external gills) may be very limited. *Macrotermes* colonies, for instance, are major components in the flow of carbon in the tropics. And coral reefs, which lie between intertidal zones and the deep of the sea, form a very rough boundary that allows for more efficient transfer of nutrients from the ocean to the coast than would be possible if no reefs were present.

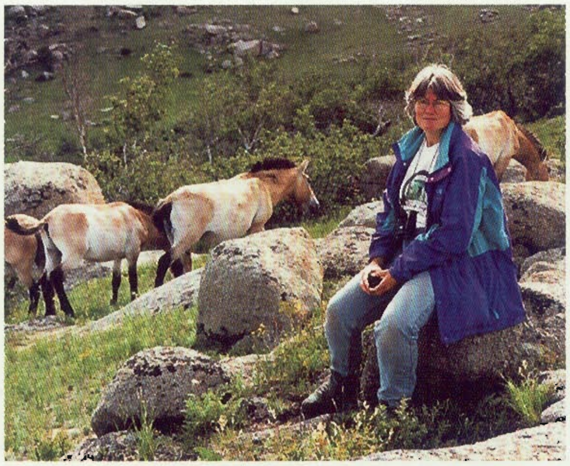
The fungi may be manipulating their insect hosts into providing them with an environment that suppresses the growth of greedy competitors.

This idea of ecosystem regulation is a controversial proposition that lies at the heart of a long-simmering argument. Some scientists—such as James Lovelock, Lynn Margulis, and other proponents of the Gaia hypothesis—maintain that the Earth is literally alive, in the same way as a nominally inanimate termite mound can be said to be alive. Nonsense, say others, how could such a world evolve? It's not Earth that evolves; it's the organisms on it that do. To say otherwise is to return to a view of living nature—purposeful and cooperative—that modern Darwinism long ago eclipsed. Hang on, say the members of a third group. Isn't this simply a return to ecology's roots as a physiological science concerned with how living things regulate flows of matter, energy, and information through ecosystems? And why, they ask, should we dismiss such questions just because they're hard to fit into our current thinking on evolution?

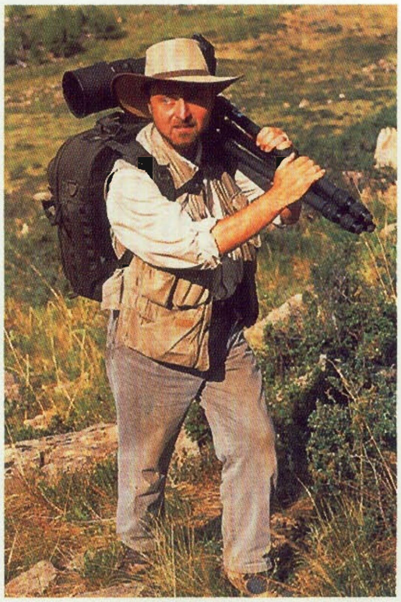
As the controversy bubbles, how about reconsidering termite colonies (or any number of other extended organisms) and asking yourself, Where does the environment end and the organism begin? I suspect the answer will not come easily to you either. ☐

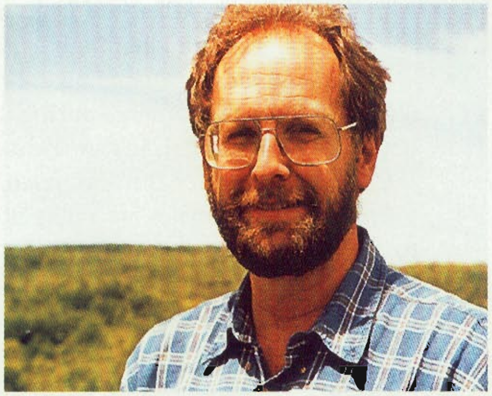
FRANS LANTING: MINDEN PICTURES

Co-op building: A mound in a Botswana forest



Lee Boyd ("Reborn Free," page 56), a professor of biology at Washburn University in Topeka, Kansas, has been studying the behavior of horses for twenty-five years. After completing a master's thesis on feral horses in Wyoming's Red Desert, she began to research captive Przewalski's horses. Boyd still observes this endangered species but is now able to do so in the horses' native land, thanks to her involvement in a project sponsored jointly by a Dutch group (the Foundation for the Preservation and Protection of the Przewalski Horse) and the Mongolian Association for the Conservation of Nature and the Environment. Veteran photographer **Frans Lanting** frequently contributes to a variety of publications, including *Natural History*. Born in the Netherlands, Lanting lives near Monterey Bay, California. For more information on the prize-winning photographer and his work, go to www.lanting.com.





J. Scott Turner ("A Superorganism's Fuzzy Boundaries," page 62) is an associate professor of biology at the State University of New York's College of Environmental Science and Forestry in Syracuse. He says he "literally stumbled across" his work on southern African termites (work that is now supported by the Earthwatch Institute) while negotiating the termite-mound-infested university campus in Mmabatho, South Africa, where he taught in 1990. Turner set about measuring gas exchange in the mounds and immediately found it was "not what the established literature said [it] should be. Thus," he reports, "began my interest." For further reading about structures of this kind, he suggests his book *The Extended Organism: The Physiology of Animal-Built Structures* (Harvard University Press, 2000), which will be released in paperback this fall.

Born in northern Israel, **Avi Klapfer** ("The Natural Moment," page 78) has lived in the United States, Costa Rica, and Palau, Micronesia. He discovered diving and boating in the Red Sea while serving in the Israeli navy but began taking underwater photos in the 1980s as a dive-boat operator in Palau. Klapfer first came upon rosy-lipped batfish in 1993, on a dive to a depth of about a hundred feet—relatively shallow for the fish but relatively deep for a human. To photograph these shy, sedentary subjects, he planned a special dive and captured the aloof individual featured in this issue after following it for half an hour. Using two underwater strobes, he took the picture with the only camera he has ever owned—a manual Nikon F-3 in Aquatica housing—and a Nikon 55mm macrolens.