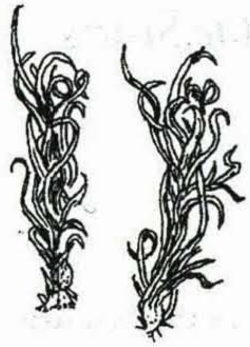
Sexual Asymmetry and the Satellite Sisters

Our local NPR station has a show in the Saturday morning lineup that usually accompanies my Saturday errands or a drive to the mountains. Sandwiched in between "Car Talk" and "What Do You Know?" is "The Satellite Sisters." "We're five sisters on two continents, with the same parents and living very different lives. Let's talk." The sisters check in by telephone from all over the world, but the show has the feel of a kitchen table, half-filled coffee cups, and a plate of sticky buns. The talk wanders from career strategies to kids, women as environmental activists, and the ethical dilemma posed by sampling grapes in the grocery store. And of course, relationships.

My husband is home puttering in the barn, my daughters are at a birthday party, and I'm feeling as contented and lazy as the Sisters' conversation this morning. Too wet to walk, too muddy to garden, the morning is mine, all mine, and I've been wanting to take a look at all these unidentified *Dicranums*. What luxury, to come to work in order to play. The rain streams down the windows of the lab and the voices of the Sisters are my only company. I can laugh out loud with them, and who will notice? There are no students, no phone calls, just some handfuls of moss and a few hours stolen from the normal hubbub of a weekend.

Dicranum is a genus of moss with many species, sisters in the same family. I think of them as only females, since the menfolk have met an unusual, and perhaps fitting, fate which strong women will understand immediately. We'll get to that later. While the Sisters trade stories of the vulnerability that comes with a new hairstyle, the exposure of a tentative self, I'm laughing at how I'd never noticed before that the *Dicranums*, more than any other moss, look like hair, combed hair, neatly parted and swept to one side. Other mosses bring to mind carpets or miniature forests, but *Dicranum* evokes hairstyles: ducktails, waves,



Dicranum montanum

corkscrew curls, and buzzcuts. If you lined them up for a family photograph, from the smallest, *D. montanum*, to the largest, *D. undulatum*, you'd definitely see the family resemblance. They all have the same hair-like leaves, long and fine with a curl at the end, brushed in one direction for that windswept look.

Like the Satellite Sisters phoning in from Thailand and Portland, Oregon, the *Dicranums* are widely distributed in forests all over the world. *Dicranum fuscesens* lives in the far north, while *D. albidum* goes all the way to the tropics. Perhaps the distance between them helps for peaceful coexistence between siblings. The genus *Dicranum* has undergone considerable adaptive radiation, that is, the evolution of many new species from a common ancestor. Adaptive radiation, whether in Darwin's finches or in *Dicranum*, creates new species that are well adapted for specific ecological niches. Darwin's finches evolved from a single ancestral species lost at sea and swept out to the barren Galapagos Islands, where the birds evolved into new species. Each island in the archipelago supports a unique species, with a unique diet. Likewise, the original *Dicranum* diverged into many different species, each with a distinctive appearance and habitat, lifestyle variations on the ancestral theme.

The force behind this divergence into new species is related to the inevitable competition between siblings. Remember wanting what your brother had, just because he had it? At the family dinner table, if everyone wants a drumstick from the Sunday chicken someone will be disappointed. When two closely related species put the same demands on their environment, with not quite enough to go around, both will end up with less than they need to survive. So, in families, siblings can coexist by developing their own preferences, and if you specialize in white meat or the mashed potatoes, you can avoid competition for the drumsticks. The same specialization has taken place in *Dicranum*. By sidestepping competition, numerous species can coexist, each in a habitat that they don't have to share with a sibling species, the mosses' equivalent of "A Room of One's Own."

Dicranum scoparium

In the *Dicranum* clan, there are family roles that could easily apply to sisters in any big family. You'll recognize them right away. *D. montanum* is the unassuming one; you know the type—nondescript, overlooked, with her short curls always in disarray. She's the one who gets the leftover habitats, the chicken wings of the Sunday feast, the occasional exposed root of a tree or bare rock. Moist shady rocks are also the habitat of the glamorous *D. scoparium*, the one who draws the looks with long, shiny leaves, tossed to one side. This is the plush *Dicranum*, the one that makes you want to run your hand over its silkiness and pillow your head in its deep cushions. When these sister species live together on a boulder, the showy *D. scoparium* takes all the best places, the moist sunlit tops, the fertile soil, while *D. montanum* fills in the gaps. No one is surprised when *D. scoparium* crowds out the little sister, invading her space and driving her to the edges.

The other *Dicranums* tend to avoid the conflicts that arise from sharing the same space, where strong identities can clash. *D. flagellare*, with leaves trim and straight, like a military buzzcut, remains aloof from the others, choosing to live only on logs in an advanced state of decay. She's the conservative one, celibate for the most part, foregoing family in favor of her own personal advancement by cloning. Solitary and intensely green, *D. viride* has a hidden fragile side, with leaf tips always broken off like bitten fingernails. *Dicranum polysetum,* on the other hand, is the most prolific mother of the family, an inevitable outcome of her multiple sporophytes. Then there's the long, wavy-leafed *D. undulatum*, capping the tops of boggy hummocks, and *D. fulvum*, the black sheep of the family; more than a dozen species of powerful females.

I'm filling a second cup of coffee and patiently cataloging the moss samples, when the Saturday conversation of the Satellite Sisters wanders to men. Some of the sisters are happily married and others are sharing last weekend's episode of looking for Mr. Right, pondering commitment and probable fatherhood personalities. Finding the right mate, a universal female concern, is also an issue for *Dicranum*. Sexual reproduction in mosses is an iffy business, as we have seen, given the limited abilities of the weak, short-lived males. Thwarted by a lack of swimmable water between them and the egg, their success depends on well-timed rainfalls. The sperm must swim to the egg, facing barriers that isolate them even though they are only a few inches apart. So near and yet so far, most eggs sit and wait in the archegonium for a sperm that never comes.

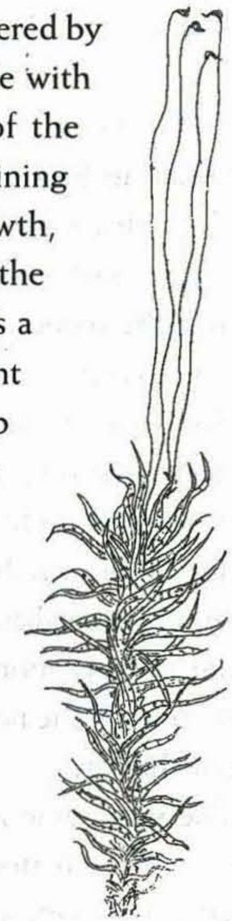
Some species have evolved a means to increase their chances of finding a mate. They become bisexual. After all, fertilization is virtually guaranteed when egg and sperm are produced by the same plant. The good news is that there will be offspring; the bad news, they are all inbred. None of the *Dicranum* species have evolved the bisexual lifestyle, keeping distinctions between the genders very clear indeed.

Dicranum fulvum

Given the difficulties in getting males and females together, it's surprising how common it is to see a colony of *Dicranum* bristling with sporophytes, the outcome of numerous sexual encounters. I have a clump of *D. scoparium* here, which must have fifty sporophytes on it, representing potentially fifty million spores. How do they do it? You might guess that the key to their reproductive success was a very favorable sex ratio, with numerous males hovering around every female. Some mosses have adopted this strategy, but not *Dicranum*.

While the radio Sisters compare their rules for first dates, I take this clump of *Dicranum* apart, looking for the macho males who are responsible for all these babies. The first shoot I pull out is a female. So is the second. And the third. Every single shoot in the colony is a female, and yet every single shoot has been fertilized. Pregnant females without a male in sight? Immaculate conception has not yet been documented in mosses, but it makes you wonder.

I slide one of the female shoots under my microscope for a closer look, and see just what I'd expect: the female anatomy, fertilized eggs swelling with the next generation. The stem is covered by a sheaf of long leaves, swept gracefully to the side with that unmistakable *Dicranum* flair. I follow one of the curving leaves along its arc, its smooth cells and shining midrib. And then I notice a whiskery little outgrowth, something I've seen only once before. Dialing up the magnification of my microscope, I can see that it's a tiny little cluster of hair-like leaves, a miniature plant growing from the massive *Dicranum* leaf like a clump of ferns growing on a tree branch. At even higher power, sausage-shaped sacs come into focus, unmistakably antheridia, swollen with sperm. Here are the missing fathers: microscopic males reduced to hiding out among the leaves of their would-be mates. They have entered female territory with a single purpose, a kind of stealthy intimacy, putting themselves so close to the females that the impotent sperm easily swim the distance to the egg.



Dicranum polysetum

Females dominate all aspects of *Dicranum* life, in numbers, in size, in energy. Whether or not males even exist lies in the power of the females. When a fertilized female produces spores, those spores are without gender. Each one is capable of becoming a male or a female, depending on where it lands. If a spore drifts to a new rock or log that is unoccupied, it will germinate and grow up to be a new full-size female. But should that spore fall onto a patch of *Dicranum* of the same species, it will sift down among the leaves of the existing females and become trapped there, where the female will control its fate. The female emits a flow of hormones which cause that undecided spore to develop into a dwarf male, a captive mate that will become the father of the next generation in the matriarchy.

The Sisters are interviewing someone on the effects of the two-career family. I want to call in to the show to see what they'd say about *Dicranum*'s domestic arrangement. Five sisters, five perspectives on dwarf males: a clear case of female tyranny, surrender of masculinity to strong women, turnabout is fair play ... hey, give them the benefit of the doubt, it's possible that they are sensitive '90's kinds of guys, giving the females their space. Will they still think that size matters?

In this time and place, men and women have the luxury of creating our relationships quite independently of their survival value to our species. Heaven knows there are plenty of us already. The ways we negotiate the balance of power and domestic harmony are unlikely to change the trajectory of our population.

But from the evolutionary perspective of *Dicranum*, the asymmetry of the sexual relationship matters a great deal. Dwarf males are an efficient solution to the problem of getting fertilized. The entire species, both sexes, benefits from this arrangement. A full-size male actually stands in the way of his own genetic success, his leaves and branches increasing the distance between sperm and egg. A dwarf male will produce many more offspring than will a full-size male. He can best contribute to the next generation by delivering sperm and then getting out of the way.

The very same impulse that propels sister species to diverge from one another creates the sharp difference between *Dicranum* males and females. Competition in a family decreases everyone's potential success. So evolution favors specialization, avoiding competition, and thus increasing the survival of the species. A large female and a dwarf male cannot compete with each other. The male is small, to better deliver sperm. The female is large to nurture the resulting sporophyte, their future, their offspring. Without competition from their mates, females get all of the good habitat, the light and water and space and nutrients, all for the benefit of the offspring.

The hour with the Satellite Sisters is winding down, with a recipe for lemon mousse. It sounds great. The rain has stopped and my mosses are done, so I turn off the radio with a smile. It's time to go home for lunch, lovingly prepared by my full-size male.

Kickapoo

I finally got around to refinishing the bottom of my canoe. After the duct tape wore off. Ahh, duct tape, the great enabler of the procrastinator. I peel it off, layer after layer, where I'd slapped it on after a collision with a rock on the Oswegatchie, and where the stern bumped down hard on a ledge of the New River. Inspecting the various cracks and chips is like taking inventory of great canoe trips. Here's a souvenir of the rapids on the Flambeau and here the gravel beds of the Raquette. Along the gunnel there is a smudge of red paint, running for six inches or so along the sky blue fiberglass. I puzzle over that one for a moment and then I remember-the Kickapoo and the summer I spent immersed.

The Kickapoo River runs through southwestern Wisconsin in a region known as the Driftless Area. The glaciers which covered the upper Midwest skipped this one little corner of Wisconsin, leaving a landscape of steep cliffs and sandstone canyons. I discovered the stream with a fellow graduate student as she surveyed the area for rare lichens. We paddled down the river, stopping at cliffs and outcrops to scan the species. All along the river I was struck by the distinctive pattern on the cliffs. The upper reaches of the cliff were spattered with lichens, but at the foot of the sheer wall were horizontal bands of moss in different shades of green, rising from the water. I was looking to find a thesis question and this one found me. What was the source of the vertical stratification that striped the cliff?

I had some ideas, of course. I'd climbed too many mountains not to notice the changes in vegetation with elevation. Elevational zonation usually results from temperature gradients and it gets cooler the higher you go. I imagined that there would be some kind of environmental gradient that changed as the cliff rose from the water, and the moss pattern would follow.

The next week I went back to the Kickapoo by myself, ready to look more closely at the banded cliffs. I put my canoe in at the bridge and paddled upstream. The current was swifter than it looked and I had to paddle hard. I maneuvered alongside the rock face, but there was nowhere to moor the canoe. Every time I stopped paddling to look at the mosses I'd be pulled downstream. I could hang on with my fingers wedged in a crack, just long enough to snatch a clump of moss, and then I'd drift away again. Any kind of systematic study was clearly going to require a different approach.

I beached the canoe on the opposite bank and decided to see if I could wade over to the cliff. The bottom was sandy and the river only knee deep. The cool water, swirling around my legs, felt wonderful on a hot day. This was starting to feel like the perfect research site. I waded over within arm's reach of the cliff. Suddenly, the bottom dropped away. The current had undercut the cliff and I found myself chest deep and clinging to the rock. But what a great face-to-face view of the mosses.

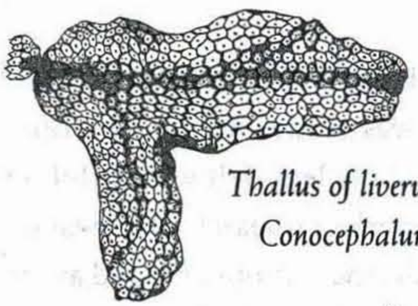
Right next to the water, extending upward for a foot or so, was a dark band of *Fissidens osmundoides*. *Fissidens* is a small moss. Each shoot is only 8 mm high, but it is tough and wiry. *Fissidens'* form is very distinctive. The whole plant is flat, like an upright feather. Each leaf has a smooth thin blade, atop which sits a second flap of leaf, like a flat pocket on a shirtfront. This envelope of leaf seems to function in holding water. All crowded together, the shoots make a rough-textured turf. *Fissidens* has well-developed rhizoids, root-like filaments that attach firmly to the grainy sandstone. At the waterline *Fissidens* formed a virtual monoculture. I saw hardly any other species, save a snail or two hanging on for dear life.

Fissidens

About a foot above water, the *Fissidens* disappeared and was replaced by assorted clumps of other mosses. Silky tufts of *Gymnostomum aeruginosum*, mounds of *Bryum* and glistening mats of *Mnium*, all are arrayed in a patchwork of different greens amidst empty patches of tawny sandstone.

Higher still, just at the limit of what I could reach from my underwater perch, began a dense mat of *Conocephalum conicum*, a thallose liverwort.

Liverworts are primitive relatives of mosses. They get their unappealing name from the botany of the Middle Ages. "Wort" is the old Anglo-Saxon word for plant. The medieval Doctrine of Signatures proposed that all plants had some use to humans and would give us a sign to reveal that use: any resemblance between a human organ and the plant would suggest it as a remedy. The leaves of liverworts are generally three-lobed, as is the human liver. There is no evidence that liverworts made effective cures, but the name has persisted for seven centuries. In the case of *Conocephalum* a better name might be snakewort, for it bears a close resemblance to the scaly skin of a green adder. This plant has no distinct leaves, just a sinuous, flattened thallus ending in three round lobes like the triangular head of a viper. Its surface is divided into tiny diamond-shaped polygons, contributing to its reptilian appearance. Closely appressed to the surface, it snakes its way over rock or soil, held loosely in place by a line of scraggly rhizoids on its underside. Brilliant green, exotic, *Conocephalum* completely covers the cliff at this height, making a striking contrast to the darker mosses below.



Thallus of liverwort
Conocephalum

I was captivated by these plants and their layered distribution on the cliff. The fact that I could paddle to my research site cinched my choice of thesis topic. The only problem was logistics. How could I make all the detailed measurements I needed while chest deep in the river? Over the next few weeks I tried lots of things. I tried anchoring the canoe and leaning out toward the cliff. The number of dropped pencils and rulers was disheartening, as was the constant threat of capsizing. I tied little Styrofoam floats to all my equipment, but the current just carried them away, bobbing merrily downstream before I could grab them. So I tethered all my gear to the thwarts of the canoe and you can imagine the resulting tangle of camera straps, data books, and light meters. Eventually, I abandoned ship and simply planted my feet on the river bottom. I devised a kind of floating laboratory with the canoe anchored beside the cliff and me standing in the river where I could reach both rocks and canoe. Data books were impossible to manage. I kept dropping them in. So I collected my measurements using a tape recorder. The machine sat securely duct-taped to the seat of the canoe and the microphone was looped around my neck. I could then have both hands free to position my sampling grids and collect specimens, and still have a free leg to snare the canoe rope when it began to drift. I felt like the one-man band of the Kickapoo. It must have made quite a picture as I was talking to myself, immersed in the river, and singing out the locations and abundance of the mosses: *Conocephalum* 35, *Fissidens* 24, *Gymnostomum* 6. I marked all the plots with dabs of red paint, which still decorates my canoe.

In the evenings I'd transcribe the tapes, converting my recorded litany to real data. I wish I'd kept some of those tapes, just for entertainment value. In between the hours of droned numbers were bursts of inspired cursing as the canoe started to drift away, tightening the microphone around my neck. I recorded any number of squeals and frantic splashes when something nibbled at my legs. I even had tape of an entire conversation with passing canoeists who handed me a cold Leinenkugels Ale as they floated by.

The vertical stratification of species was very clear with *Fissidens* at the bottom, *Conocephalum* at the top, and a variety of others sandwiched in between. But my hypothesis about the cause of the pattern was not supported. There were no significant differences in light, temperature, humidity, or rock type along the face of the cliff. The pattern had to be caused by something else. Standing in the river day after day, I was becoming vertically stratified myself—shrivelled toes at the bottom, sunburned nose at the top, and muddy in between.

Oftentimes, an abrupt pattern in nature is caused by an interaction between species, such as territorial defense or one tree species shading out another. The pattern I was observing might well be the result of some competitive "line in the sand" between *Conocephalum* and *Fissidens*. I gave the two species a chance to tell me about their relationship, by growing them side by side in the greenhouse. Alone, *Fissidens* did fine. *Conocephalum*, likewise. But when they were grown together there was clear evidence of a power struggle, which was consistently lost by *Fissidens*. Time after time, *Conocephalum* extended its snaky thallus over the top of diminutive *Fissidens*, completely engulfing it. Their separation on the cliff became clearer. *Fissidens* had to keep away from the liverwort in order to survive. But, if competition was so important, why didn't *Conocephalum* grow all the way to the waterline and simply obliterate the other species?

One day in late summer I noticed a wad of grass snagged on a branch high above my head—a high-water mark. Clearly the river was not always at wading depth. Perhaps the vertical stratification was due to differences in how the species tolerated flooding. I collected clumps of each species and submerged them in pans of water for various times: 12, 24, 48 hours. The *Fissidens* remained perfectly healthy even after three days, as did *Gymnostomum*. But after only 24 hours the *Conocephalum* was black and slimy. So here was a piece of the pattern. *Conocephalum* must be confined to the higher levels of the cliff by its inability to withstand flooding.

I wondered how often floods like the one I'd simulated actually happened. Could it be often enough to create a barrier for *Conocephalum*'s expansionist tendencies? As luck would have it, the Army Corps of Engineers was wondering the same thing, albeit for a different reason. They were considering constructing a flood-control dam on the river and had installed a gaging station at the bridge below my cliffs. They had amassed five years of daily measurements of water levels on the Kickapoo. I could use their data to calculate the frequency with which any point on the cliff had been underwater. I could also call in to the automated phone number to learn the current water level at the bridge. I've not been much of a cheerleader for the Corps, given their propensity for spoiling rivers, but these data were invaluable.

All winter long I analyzed the data to match them to the distribution of mosses on the cliff. Not surprisingly, the gaging station data matched the elevational zonation of the bryophytes very well. The water level was most frequently lapping at the base of the cliff where *Fissidens* dominated the vegetation. It was tolerant of flooding and its wiry streamlined stems allowed it to withstand the frequent company of the current. Flood frequency declined with rising elevation on the cliff. The zone dominated by loosely attached *Conocephalum* was inundated very rarely. High above the water, *Conocephalum* could safely spread its snaking thallus over the rock in an uninterrupted blanket of green. One species dominated where flood frequency was high. Another species dominated where disturbance was low. But what about in the middle? Here was a tremendous variety of species, as well as patches of open rock as bare as a billboard advertising "space available." In the zone of intermediate flood frequency no one species dominated and diversity was high. As many as ten other species were sandwiched here between the two superpowers.

At the same time as I was wading the Kickapoo, another scientist, Robert Paine, was exploring a different gradient of disturbance frequency, wave action on the rocky intertidal zone of the Washington coast. He was looking at communities of algae, mussels, and barnacles, which may seem to have little in common with mosses. And yet both are sessile, attached to rock and engaged in a competition for space. He observed an intriguing pattern—-few species lived where the wave action was constant and fewer still lived on rocks which were virtually undisturbed. But in between, where disturbance was intermediate in frequency, species diversity was extremely high.

The rocky coast and the Kickapoo cliffs helped to generate what has become known as the Intermediate Disturbance Hypothesis, that diversity of species is highest when disturbance occurs at an interval between the extremes. Ecologists have shown that in the complete absence of disturbance, superior competitors like *Conocephalum* can slowly encroach upon other species and eliminate them by competitive dominance. Where disturbance is very frequent, only the very hardiest species can survive the tumult. But in between, at intermediate frequency, there seems to be a balance that permits a great variety of species to flourish. Disturbance is just frequent enough to prevent competitive dominance and yet stable periods are long enough for successional species to become established. Diversity is maximized when there are many kinds of patches of all different ages.

The Intermediate Disturbance Hypothesis has been verified in a host of other ecosystems: prairies, rivers, coral reefs, and forests. The pattern it reveals is at the core of the Forest Service's policy on fire. Fire suppression with Smokey Bear's vigilance produced a disturbance frequency which was too low and the forests became a monocultural tinderbox. Too high a fire frequency left only a few scrubby species.

But like Goldilocks and the Three Bears (one must have been Smokey himself), there is a fire frequency which is "just right," and here diversity abounds. Creation of a mosaic of patches by mid-frequency burning creates wildlife habitat and maintains forest health, while fire suppression does not.

When the ice went out on the Kickapoo the next spring I called the gaging station and an electronic voice informed me that the river was in flood. So I jumped in my car and drove down to see what the mosses looked like now. The river was chocolate brown with dissolved farmland. Logs and old fenceposts were pushed along in the torrent, bumping against the cliff. My red paint markers were nowhere to be seen. By the next morning the waters had receded as quickly as they had come and the aftermath was revealed. The *Fissidens* had emerged unscathed. The mid-level mosses were sodden with mud and battered by the logs and the pull of the water. A few more bare patches had been made. The *Conocephalum* had not been submerged long enough to die, but it was torn away in great swaths, hanging from the cliff like ripped wallpaper. Its flat loose form had made it particularly vulnerable to the pull of water, while *Fissidens* was unaffected. The open patches created by the removal of *Conocephalum* made temporary habitats for a new generation of mosses which would persist there until *Conocephalum* gathered its strength and returned. These are the species which are not able to compete with *Conocephalum*, nor to withstand the frequent flooding. They are fugitives between two forces, living in the crossfire between competition and the force of the river.

I like to think of the satisfying coherence in that pattern. Mosses, mussels, forests, and prairies all seem to be governed by the same principle. The apparent destruction of a disturbance is in fact an act of renewal, provided the balance is right. The Kickapoo mosses had a piece in telling that story. Sandpaper in hand, I look at the splotch of red paint on this old blue canoe and decide to let it be.

Choices

My neighbor, Paulie and I communicate mostly by shouting. I'll be outside unpacking the car and she'll stick her head out of the barn and yell across the road, "How was your trip? Big rain while you were gone, the squash in the garden are going crazy—help yourself." Her head pops back into the barn before I can answer. She takes a dim view of my gallivanting around, but keeps a good eye on the place while I'm gone. While I'm out stacking firewood or planting beans, I'll catch sight of her blaze orange cap and call across the road to her with news of a downed fenceline I discovered up by the pond. Our shouts carry the shorthand affection we have for each other. Over the years it's been a telegraph from my side of the road to hers, carrying messages of kids growing up, parents growing old, breakdowns of the manure spreader, and news of the killdeer nesting in the pasture. On 9/11 I ran from my TV to the barn where we hugged and cried for a short moment until the feed truck arrived and brought us back to the immediate need of calves to be fed.

My old house and her old barn, in the little town of Fabius, New York, were once part of the same farm, starting way back in 1823. They share the shade of the same big maples and are watered by a common spring. We've brought them back from the brink of decay together, so it's fitting that we, too, are friends. Sometimes, when the weather is nice, we stand with arms folded in the middle of the road to talk, shooing barn cats out of the road and holding up traffic, which consists of the occasional haywagon or the milk truck. Our dirty work gloves are pulled off as we soak up the sun and the talk and are pulled back on again as we turn away. On the rare occasions when we do talk on the phone she forgets she's not hollering from the barn and I have to hold the phone a foot from my ear.

As observant neighbors we know a lot about each other. She just shakes her head and laughs over my field seasons spent earnestly investigating the reproductive choices of mosses. All the while she and her husband Ed are milking 86 head, raising corn, shearing sheep, and building a heifer barn. Just this morning, we met down at my mailbox and had a moment to talk while she was waiting for the AI man. "Artificial Intelligence?" I asked with a raised eyebrow. This cracked her up, one more sign of the detached ignorance of her neighbor, the professor. The white panel truck splashed over the potholes to the barn, a picture of a bull on the side. "Artificial Insemination," she shouted over her shoulder as we walked back into our worlds on opposite sides of the road. "Your mosses may have reproductive choices, but my cows sure don't."

Mosses do exhibit the entire range of reproductive behaviors from uninhibited sexual frenzy to puritanical abstention. There are sexually active species churning out millions of offspring at a time and celibate species in which sexual reproduction has never been observed. Transexuality is not unheard of; some species alter their gender quite freely.

Plant ecologists measure a plant's enthusiasm for sexual reproduction with an index known as reproductive effort. This measure is simply the proportion of the plant's total body weight which is dedicated to sexual reproduction. For example, our maple tree allocates much more of its energy to production of wood than to its tiny flowers and helicopter seeds that twirl to the ground on the breeze. In contrast, the dandelion in the pasture has a very high reproductive effort, with much of the plant's mass tied up in yellow flowers, followed by drifts of fluffy seeds.

The energy allocated to reproduction can be spent in a variety of ways. The same number of calories could be used to make a few large offspring that the parents invest in heavily. Alternatively, some are more profligate, spending their energy on a large number of tiny, poorly provisioned offspring. Paulie has strong opinions on those who have children that they don't adequately support. One of the barn cats, a long-haired beauty named Blue, seems to take the attitude that kittens are a disposable commodity. She has litter after litter, but can't be bothered to nurse them and leaves them to fend for themselves. Mosses like *Ceratodon* take the same approach. On a patch of disturbed ground along the cow track to the barn, the leaves of *Ceratodon purpureus* are barely visible under the dense swath of sporophytes it produces all year long. But each spore is so small and poorly provisioned that, like Blue's kittens, it has a vanishingly small chance of surviving. Fortunately, there is among the barn cats a paragon of good mothering, Oscar. She's the old lady of the haymow, and carefully tends her single litter, and willingly adopts Blue's orphans as her own. For this, Oscar earns a place at the milk dish at milking time.

Paulie would approve of a moss like *Anomodon*, growing on the shaded rock wall behind the barn. This species delays its spore production until later in life, preferring to allocate its resources to growth and survival, rather than unfettered reproduction.

The two strategies of high and low reproductive effort are usually associated with a particular environment. In an unstable, disturbed habitat, evolution will tend to favor those species that produce many small highly dispersable offspring. The unpredictable nature of the habitat, like the *Ceratodon* near a cow path, means that the adults have a high risk of dying by disturbance, and so it is advantageous to reproduce quickly and send your progeny off to greener pastures. The destination of those wind-blown spores is unknown, but is likely quite different from the path edge of the parents. Sexual reproduction also conveys a strong advantage by mixing up the parents' genes into new combinations. Every spore is like a lottery ticket. Some will be good combinations, some will be bad, but the gamble pays off with millions of offspring spread randomly over the landscape. One will surely find a patch of ground where its novel genetic formula will bring it success. Sexual reproduction creates variety, a distinct advantage in an unpredictable world. However, sexual reproduction also incurs some costs. In creation of egg and sperm, only half of the parents' successful genes are passed to the offspring, and those genes are shuffled in the lottery of sexual reproduction.

In her muddy boots and manure-spattered jacket, Paulie doesn't fit the white-coat image of genetic engineering, and yet she is working at the forefront of its application. A Cornell grad, she has bred an award-winning herd of Holsteins with impeccable genetic pedigrees. Rather than lose this hard-won genetic advantage by mating her best cows with any old bull, she is using artificial insemination and then transferring the identical embryos to surrogate mothers in the herd. In this way, she will develop a herd with little variability, perpetuating the successful genotypes that would have been scrambled by ordinary sexual reproduction. Such cloning is a recent development in dairy production, but mosses have been doing it since the Devonian era.

Reproductive strategies that limit variation and preserve the parents' favorable gene combinations are commonplace among the mosses. The rock wall behind the barn has been undisturbed since the first farm owners built it 179 years ago. In such a steady, predictable habitat a steady, predictable way of life is most successful. The *Anomodon* mat that lives there has had nearly two centuries to prove that it bears a genetic makeup well suited to that particular spot. Energy devoted to frequent sexual reproduction would essentially be wasted here, by producing wind-blown spores of potentially unfit genotypes, which would simply be lost on the wind. In a stable, favorable environment, it is better to invest that energy in growth and clonal expansion of the existing long-lived moss, preserving the tried and true genotype, like pedigreed cows.

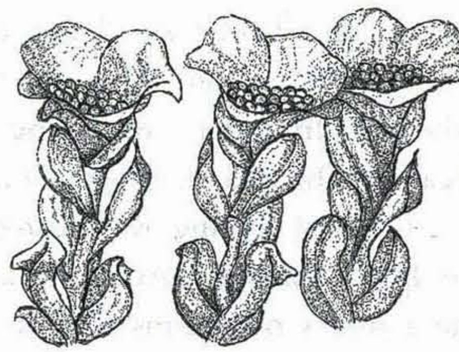
Natural selection is constantly acting upon the pool of individuals that make up a population, and only the most fit survive. Burying generations of barn cats who never learned to cross the road, or stillborn calves, clearly reveals the hand of natural selection. On such occasions, Paulie brushes off the loss with a practiced line. "If you're going to have livestock, you're going to have deadstock." Despite her bluster, Paulie's menagerie tells a different story. Not all of her animals are the cream of the crop. One stall is home for an old cow, blind now for many years. Her name is Helen. She's a good old girl and with the time-honored nose-to-tail guidance system she stills goes out to pasture with the others. And then there's Cornellie, the orphaned lamb whom Paulie brought home in diapers to sleep by the woodstove until it was big enough to survive. But, in nature, there is rarely a Paulie who spares the unfit from the scythe of natural selection. So I've been looking at the reproductive choices made by mosses in light of natural selection. Which choices result in survival and which are steps toward extinction?

Chance and our choices have brought Paulie and I together, converging for some reason on this old hill farm. Something about the way the house nestles in the hill sheltered from the wind, or the way the morning sun pours over the meadow. She fled the expectations of Boston family and chose the intense flavor of farming over a career as an animal physiologist. I flew here like a homing pigeon after a sad divorce with the fervor to start again, on my own terms. Our dreams have found a home here. Paulie recreates her self-sufficiency every single day and revels in the company of animals. And here my microscopes can share the table with blackberry pies.

Up in the hemlock swamp at the top of our pasture, the woods are fenced from grazing. Paulie is mowing hay in the adjacent field, the tractor rumbling along. I wave to her as I duck under the barbed wire and into the woods. A few steps into the trees and a hush descends with the green filtered light. The hemlock timbers which built my house and Paulie's barn were cut here generations ago. The old logs and decaying stumps are covered with one of my very favorite mosses, *Tetraphis pellucida*. I know of no moss more charged with well-being than *Tetraphis*. Its young leaves are luminous as dewdrops and swollen with water. The species epithet "*pellucida*" reflects this watery quality of transparency. Its sturdy little shoots are clean and simple and stand upright in a hopeful sort of way. Each stem is no more than a centimeter tall with a dozen or so spoon-shaped leaves arranged like an open spiral staircase ascending the stem.

In contrast to most mosses, which have adopted a particular lifestyle and stuck with it, *Tetraphis* is remarkable for its flexibility in making reproductive choices, sexual and otherwise. *Tetraphis* is unique in having specialized means of both sexual and asexual reproduction, standing in the middle of the road of reproductive options.

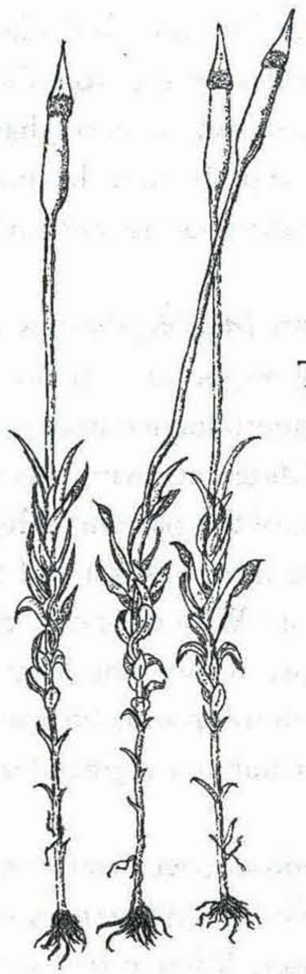
Most mosses have the ability to clone themselves from broken-off leaves or other torn fragments. These bits of debris can grow into new adults that are genetically identical to the parents, an advantage in a constant environment. The clones remain near the parents and have little ability to venture into new territory. Cloning by dismemberment may be effective but it is a decidedly crude and random way to send genes into the future. *Tetraphis* however, is the aristocrat of asexual



Gemmae cups of Tetraphis pellucida

reproduction, possessed of a beautifully sculpted design for cloning itself. When I kneel to look closely at the patches of *Tetraphis* on the old stumps, I see that the surface of the colonies is sprinkled with what look like tiny green cups. These gemmae cups, formed at the ends of the upright shoots, resemble miniature bird's nests, complete with a clutch of tiny emerald eggs. The nest or gemmae cup is a circular bowl made of overlapping leaves and nestled within it lie the egg-like gemmae. Each gemma is a roundish mass of only ten to twelve cells, which catch the light and shimmer. Already moist and photosynthesizing, each gemma is poised to establish itself as a new plant, cloned from its parent. It rests in the nest, waiting. Waiting for an event that will propel it away from its parent, where there's room to grow and start its own family.

When the skies darken and the thunder rolls, the time is at hand. Great big raindrops pelt the forest floor, and ants and gnats dive into mosses for shelter, lest they be squashed by the momentum of the raindrops. But sturdy little *Tetraphis* waits expectantly, for it is designed to harness the power of a raindrop. When a gemmae cup receives a direct hit, the raindrop breaks loose the gemmae and propels them outward, leaving the nest empty. The gemmae can be splashed up to fifteen centimeters away, which isn't bad for a plant only one centimeter tall. In a favorable location, the gemmae can regenerate an entire new plant in the span of a single summer. In comparison to spores, which are at the mercy of a fickle breeze that deposits them anywhere, a rock or a rooftop or the middle of a lake, gemmae are more likely to land in the same neighborhood as their parents. As clonal propagules, the gemmae carry a combination of genes that has already proven successful on this stump.



Sexual shoots of Tetraphis pellucida bearing sporophytes

In contrast, the spores produced by the sexual mixing of the parents' genes are a myriad of genetic combinations, a powder of potential sent off to seek its fortune in the unknown realm beyond the stump. There are other patches of *Tetraphis* on the very same stump which are the cinnamon color of old redwood. They take their rusty tint from the dense swath of sporophytes which rise from the green shoots below. Each sporophyte ends in a capsule shaped like an open jar. The mouth of the jar is ringed with four rusty teeth, from which the name *Tetraphis* ("four teeth") is taken. When the capsule is ripe, millions of spores will be released onto the breeze. The product of sex, the spores will carry the shuffled genes far from their parents. While these spores have the advantage of variety and distance, their success rate is exceedingly small. The tiny spores, even when carefully sown on a suitable site like another hemlock stump, yield only one plant for every 800,000 spores sown. There is clearly a tradeoff between size and success. The gemmae are hundreds of times larger than spores, and hundreds of times more effective in generating new plants. The large size and active metabolism of the gemmae, in comparison to spores, give them a higher chance of success. In experiments, I've found that one in ten gemmae survive to establish a new plant.

I can hear that the sound of the hayrake has stopped and Paulie comes down the sun-dappled path to see what I'm up to, grateful for a respite from the summer sun. I hand her my water bottle and she drinks deeply, wiping her mouth on the back of her hand and bending down to sit on a hemlock stump. I show her the two kinds of *Tetraphis*, the asexual colonies with reliable "stay at home" gemmae and the highly sexual colonies, sending their adventurous offspring off on the breeze.

She just nods her head and laughs. It's a story she knows very well. Her daughter, so very like her mother, has decided to stay on and work the land alongside her parents after college. Her oldest son, however, has flown the nest to become a teacher at the other end of the state, having no interest at all in days that start with milking before sunrise and end long after the cows come home.

When I look at logs and stumps covered with *Tetraphis*, there is a striking pattern. The two forms, gemmae and spores, occur in distinct patches, almost never intermingling. Since each reproductive strategy, clonal and sexual, is usually associated with a very different environment and with individual species, I wonder at the cause of this pattern. Why should the same species adopt a clonal lifestyle in one patch and a sexual lifestyle in another on the very same stump? Why does natural selection allow two opposite behaviors to coexist in the same plant? This question led me into a long and intimate relationship with *Tetraphis*, one of fascination and of respect where *Tetraphis* taught me a great deal about doing science.

I suspected right away that the cause of the reproductive patchiness was some aspect of the physical environment. Perhaps differences in moisture or nutrients in the decaying wood caused different forms of reproduction. So I laboriously measured environmental factors to see which one was correlated with either sexual or clonal behavior. I lugged around a pH meter, a light meter, a pyschrometer, and bagged samples of decaying log to take back to the lab for an analysis of moisture and nutrients. Months of expectant data analysis later, I discovered that there was no correlation whatsoever. There seemed to be no rhyme nor reason to *Tetraphis'* reproductive choice. But if there's anything that I've learned from the woods, it's that there is no pattern without a meaning. To find it, I needed to try and see like a moss and not like a human.

In traditional indigenous communities, learning takes a form very different from that in the American public education system. Children learn by watching, by listening, and by experience. They are expected to learn from all members of the community, human and non. To ask a direct question is often considered rude. Knowledge cannot be taken; it must instead be given. Knowledge is bestowed by a teacher only when the student is ready to receive it. Much learning takes place by patient observation, discerning pattern and its meaning by experience. It is understood that there are many versions of truth, and that each reality may be true for each teller. It's important to understand the perspective of each source of knowledge. The scientific method I was taught in school is like asking a direct question, disrespectfully demanding knowledge rather than waiting for it to be revealed. From *Tetraphis*, I began to understand how to learn differently, to let the mosses tell their story, rather than wring it from them.

Mosses don't speak our language, they don't experience the world the way we do. So in order to learn from them I chose to adopt a different pace, an experiment that would take years, not months. To me, a good experiment is like a good conversation. Each listener creates an opening for the other's story to be told. So, to learn about how *Tetraphis* makes reproductive choices, I tried to listen to its story. I had understood *Tetraphis* colonies from the human perspective, as clumps in various stages of reproduction. And I had learned little by doing so. Rather than looking at the clump as an entity, I had to recognize that the clump was simply an arbitrary unit that was convenient for me, but had little meaning for the moss. Mosses experience the world as individual stems and to understand their lives I needed to make my observations at the same scale.

So I began the laborious work of inventorying the individual shoots in hundreds and hundreds of *Tetraphis* colonies. I took pains to see every patch of *Tetraphis* I sampled as a family of individuals. Every single stem was counted, and every shoot was categorized by its gender, its stage of development, and its mode of reproduction, gemmae or spores. I wonder how many shoots I've counted in all—probably millions. A dense colony of *Tetraphis* can have three hundred shoots per square centimeter. And then each colony was marked. I found that the plastic cocktail swords which impale olives in martinis make the best markers. They won't decay and the bright pink plastic makes them easy to locate the next year. And besides, I like to imagine the conversations of hikers who encounter mossy logs decorated with swizzle sticks.

The next year, I went back and found each of the marked colonies and counted them again. In notebook after notebook, I recorded the changes in their lives. And then again the year after that. Slowly, with my knees in the duff and my nose on the stump, I was starting to think like a moss.

I think that Paulie would be the first to understand this. Making a living as a dairy farmer on a few hilly acres is a tough proposition. She has been successful because she knows her herd, not as a clump, but as individuals. There's not a numbered ear tag on the farm; she knows every cow by name. She can spot when Madge is ready to calve, just by the way she walks down the hill. The time spent to know their habits and their needs gives her a competitive edge over the industrial-scale dairy farmers.

My notebooks record the fate of each patch, a changing census of the tiny moss community. With patient watching, and no direct questions, year by year, *Tetraphis* began to tell its own story. Colonies on bare wood start out with sparse and widely scattered shoots, a community with plenty of elbow room. In these low-density patches of fifty individuals in a square-centimeter sample, virtually every shoot bears a gemmae cup at its tip. The falling gemmae grow into more thrifty young shoots and by the time I return the next year the stems have gotten crowded. In colony after colony, I notice a remarkable pattern. With crowding, the gemmae disappear. There is an abrupt switch from making gemmae to making female shoots. Crowding seems to trigger the onset of sexual reproduction. With a populous colony of females and scattered males, it's not long before sporophytes appear. The colony has transformed itself from the vibrant green of gemmiferous shoots to the rusty color of spore production. When I return the next year, the colony has become even more crowded, approaching three hundred stems per square centimeter. This high density seems to trigger a radical shift in sexual expression. Now, the only shoots produced are male, with not a female or a gemmiferous shoot in sight. We discovered that *Tetraphis* is a sequential hermaphrodite, changing its gender from female to male as the colony gets crowded. This switching of gender with population density had been observed in certain fish, but never before in mosses.

In trying to piece together *Tetraphis'* story, I wanted to be sure that I understood what was going on, that the choice of having sex or making gemmae was really determined by the density of the colony. If that were true, then if I could change the density, the mosses should change behavior. Perhaps I could ask an indirect question, and perhaps they would answer. To ask the question in the language of mosses, I took a cue from Paulie's woods.

A few years ago, when she needed cash for the new heifer barn, she decided to harvest some trees from her woodlot. She shopped around carefully for a logger committed to low-impact harvest, someone who would take good care of the woods. They cut timber in winter, scattering their openings, and made a clean job of it. In the springs that followed, the thinned woods had a carpet of snowy white Trillium and yellow trout lilies blooming under the leafy canopy. The lowered density had let in more light and rejuvenated the old stand.

Like a logger in miniature, I sat poised with fine forceps over the old, dense *Tetraphis* patches. One by one, I plucked out single shoots of *Tetraphis*, stem by stem, until the density was reduced by half. And then I let them be, returning the next year to observe if they had given me an answer to my question. The unthinned patches of *Tetraphis* remained male and had started to turn brown. But the patches where I'd opened the moss canopy by thinning were green and vibrant. The holes I'd made in the *Tetraphis* turf were being filled with thrifty young shoots, bearing gemmae cups at their tips. The mosses had answered, in their own way. Low density is a time for gemmae, high density for spores.

The transformation to being male appears to have adverse consequences. Over and over, I observed that the dense male patches were starting to die back, becoming dry and brown. These tired male colonies, spent with reproduction, were then easily invaded by other mosses on the log. Sometimes, I'd find the telltale swizzle sticks in a patch where old male colonies of *Tetraphis* had disappeared, obliterated by the advance of carpet mosses. Why would *Tetraphis* adopt a sexual lifestyle that seemed to doom it ultimately to fail, headed for local extinction?

On many occasions, I'd return to a familiar stump only to find that the carefully marked patch of *Tetraphis* had vanished. In its place was a clean, bare surface of newly exposed wood. Scrambling around on my knees, I found the patch of *Tetraphis*, still impaled by its cocktail sword, at the base of the stump, where it had tumbled in a small avalanche of decayed wood. These stumps and logs were a landscape in motion. The process of decay and the activity of animals were constantly causing the logs to fall away, piece by piece. The stumps looked like small mountains, forested by mosses, with a talus slope of decayed chunks lying like fallen boulders at their base. Blocks of old wood fell away, carrying their surface cover of *Tetraphis* and creating the bare places I'd noticed. And what became of such open spaces, these patches of new wood? Looking closely, I could see that they were sprinkled with gemmae, little green eggs that had splashed into the gaps in the old *Tetraphis* cover. In the aftermath of disturbance, the seeds were sown for the next wave of *Tetraphis*.

When I stop by the barn to buy a carton of fresh brown eggs, Paulie is just coming back from a meeting. We stand there in the sun, admiring the morning glories climbing up the side of the old silo. She heard some talk of opening a casino over in the next county and we laugh about the unwary throwing their money away on chance. "Heck," she says, "we don't have to go to the casino to gamble. Farming is like blackjack, year in and year out." Milk prices are notoriously unreliable, and feed costs can triple from one year to the next. Farm income can fluctuate like clouds passing over the sun, but college tuition only goes up. That's where the Christmas trees come in, and the sheep and the feed corn. To buffer against uncertainty, Ed and Paulie run a diversified farm. The cows are the mainstay but in years when milk prices are down, maybe the lamb market will pay the kids' tuition, or maybe the Christmas trees. They survive in an era of disappearing family farms by a resilience rooted in flexibility, where stability comes from diversity.

It's the same for *Tetraphis*, a moss that is hedging its bets in an unpredictable landscape where a landslide of decay can disrupt years of steady growth. It achieves stability in an unstable habitat by freely switching between reproductive strategies. When the colony is sparse and there is lots of open space, it pays to be clonal. The gemmae can occupy the bare wood more quickly than any spore and maintain a competitive advantage against other moss species. But when it gets crowded, the only offspring that have a chance are spores. And so sexual reproduction is begun, to produce spores of divergent genetic makeup that will be blown away from the parents in their dwindling habitat. It's a gamble that any spore will land on a suitable log and be able to start a new colony. But it's a sure thing that without disturbance the colony will become extinct if it stays in one place.

The other mosses of less imaginative reproduction are slowly creeping closer, ready to engulf little *Tetraphis*. But *Tetraphis* has chosen its habitat well, taking full advantage of the rot which reliably causes disturbances to the log. Just about the time that the spent colony of *Tetraphis* is about to succumb to competitors, the face of the log peels away in a landslide of decay, exposing fresh new wood as it eliminates a patch of competitors and *Tetraphis* as well. If *Tetraphis* had to rely on spores to colonize these open spaces, its competitors would more often win the race for space. But just a few centimeters away stands a patch of *Tetraphis* in its clonal phase. With the next rain, gemmae are splashed into the opening and rapidly produce a new patch of vibrant green shoots. Decay renews the open space, and in accord, *Tetraphis* renews itself. *Tetraphis* plays both sides of the game, producing gemmae for short-term profit and spores for long-term advantage. In this changeable habitat, natural selection favors flexibility rather than commitment to a single reproductive choice. Paradoxically, those species adapted to a specialized lifestyle come and go, but *Tetraphis* persists by keeping its options open and maintaining its freedom of choice.

Maybe it's the same with our old farm, persisting now for almost two centuries. Generations of other women before us have shooed barn cats out of the road, planted lilacs, and raised their children under these maples. The old bull has been replaced by the AI man, and the cistern by a well. But the world is still unpredictable and still we survive by the grace of chance and the strength of our choices.