

Water-Pollinated Plants

Once thought to be mere aberrations of nature, these flowering aquatic species provide evidence for the evolutionary convergence toward efficient pollination strategies

by Paul Alan Cox

On a sunny October day in 1787, the botanist Filippo Cavolini rowed a boat in the Bay of Naples, continuing a pursuit that had so far proved futile. Four years previously, divers had brought him a species of eelgrass, *Zostera marina*, that bore fruit. Cavolini had immediately realized that the plant was special: it must flower, unlike the seaweeds and other marine algae he had collected. But he had yet to discover its blossoms. Cavolini's quest finally ended that day as he reached a *Zostera* population that grew in the bay. He became tremendously excited to find "a spike [flower cluster] not unlike that of a grass floating on the water."

Later, examining the pollen under his laboratory microscope, Cavolini was stunned to see that the grains were not small and round, like those of terrestrial plants: "I found it [the *Zostera* pollen] different from that of other plants, being oblong like little eels, which, with a sudden and brisk motion, exploded and scattered their sperm in a twinkling of an eye." Based on this observation, he drew a startling conclusion: *Zostera* must reproduce by pollination in the open water.

Cavolini's discovery was remarkable. Because water causes the pollen of terrestrial plants to burst, botanists had regarded the aquatic environment as inimical to pollination. Pollen, which transports and protects a plant's genetic information, is a necessary adapta-

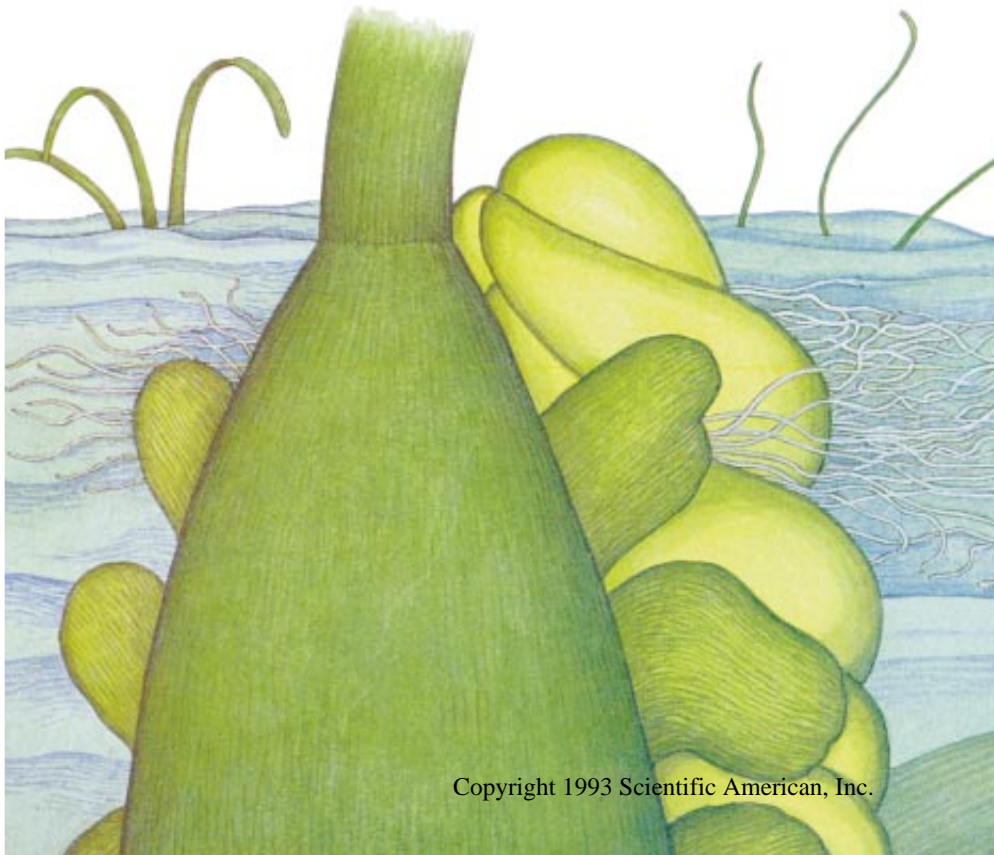
tion for flowering plants on land. These plants use wind and animals to disseminate their gametes over dry terrain.

But Cavolini's finding of water as a pollination vector has recently been reconsidered in light of search theory and diffusion physics. The results indicate that hydrophilous, or water-based, pollination systems cannot be considered mere quirks of natural history, as previously thought. Rather water-pollinated plants should now be viewed as compelling cases of convergent evolution, because unrelated hydrophilous species have evolved similar strategies that promote efficient pollination. Although they are uniquely adapted to their watery environment, their ancestors can be ultimately traced to flowering plants

that reinvaded the water. Hydrophilous plants thus retain many features of the reproductive systems of their terrestrial counterparts, such as whales and porpoises kept their mammalian traits after their return to the ocean.

Water pollination should not be confused with reproduction in such nonflowering plants as algae, ferns, mosses and liverworts. Although these species require water—say, dewdrops or water-fall spray—they do not produce pollen; they simply disperse their motile gametes into the water. Nor is hydrophilous pollination similar to the aerial pollination of other aquatic flowering plants, such as water lilies, that raise their flowers above the surface to where insects or wind can pollinate them.

MALE FLOWER of the surfgrass *Phyllospadix scouleri* (left) releases filamentous pollen that forms snowflakelike rafts. Currents carry the pollen mass to female flowers (right), where the pollen grains contact the stigma, resulting in fertilization.



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Not uncommon taxonomically or geographically, water-pollinated species occur in 31 genera in 11 different families. They range in latitude from northern Sweden to southern Argentina and in altitude from 40 meters below sea level to 4,800 meters high in the Andes, where *Elodea potamogeton* impedes navigation on Lake Titicaca on the Peru-Bolivia border. They are ecologically diverse as well, extending from tropical rain forests to seasonal desert pools. Freshwater species feed fish and wildfowl, whereas marine species support sea turtles, manatees and shellfish.

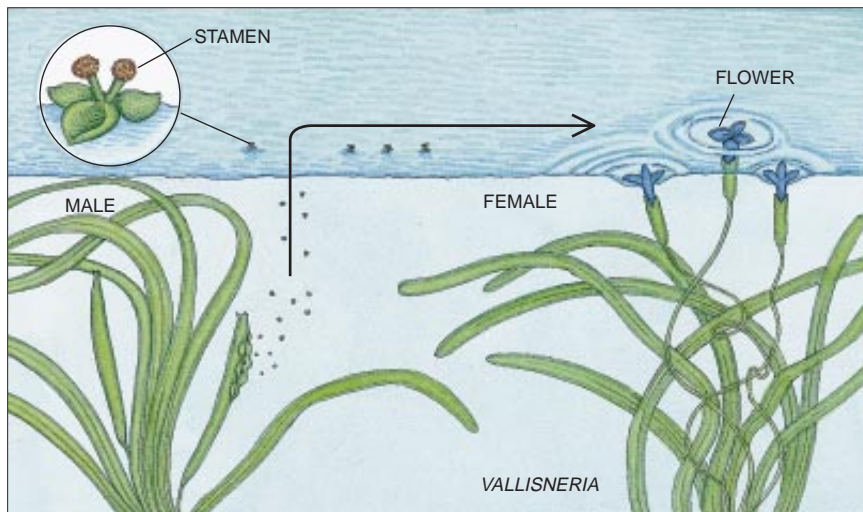
How do hydrophilous plants successfully use water as a pollination vector? Water would appear to be a poor medium in which to disperse pollen. In addition to its propensity to cause most pollen grains to burst, water can be unpredictable. Currents can be quite erratic, and tides can abruptly submerge plants or leave them far above the surface.

Historical accounts provide some information about how the plants exploited the water. Erasmus Darwin, grandfather of Charles Darwin, described the remarkable pollination system of the freshwater plant *Vallisneria* more than two centuries ago. (Darwin's description was so compelling that the Reverend William Paley cited it as evidence for

the existence of God in his influential book *Natural Theology*.) Darwin found that the submerged male plants release flowers that float to the surface. Once there, the petals recurve, elevating the flower on a meniscus of water that enables it to glide with the slightest breeze. Two sterile anthers function as tiny sails, while two fertile anthers hold the spherical pollen of *Vallisneria* aloft. Each floating female flower, anchored by a long stalk to the bottom of the pond, creates a slight depression in the water's surface. As the male flower falls into the depression created by the female flower, it transfers pollen to the stigma, thus effecting pollination.

In 1792 Cavolini expanded on his earlier studies of *Zostera*, showing that another mechanism—directly releasing pollen into the water—existed for flowering aquatic plants. Cavolini also reported a second sea-grass species, *Cymodocea nodosa*, that releases its noodlelike pollen directly onto the surface of the water. He wrote that “white capillary pollen... covered for a great space the surface of the water around.” Such pollen was protected from bursting because it could rapidly equilibrate with the seawater.



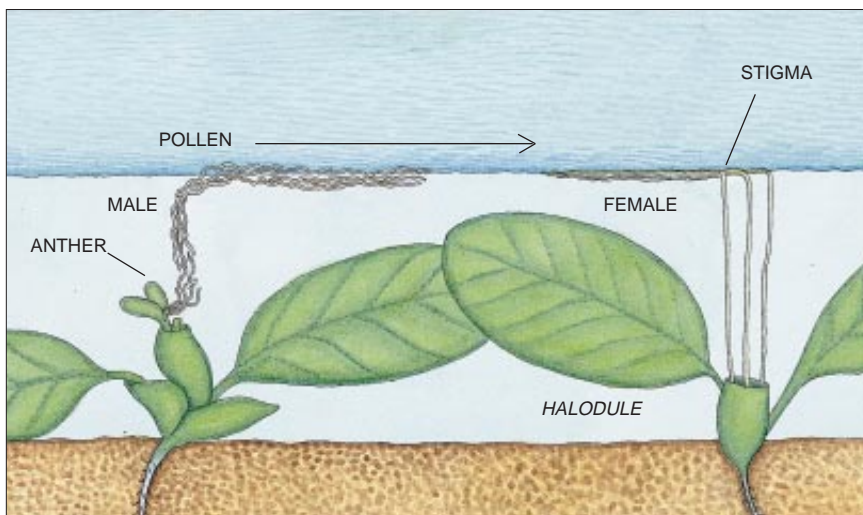


ABOVE-SURFACE POLLINATION is one reproductive strategy that hydrophilous, or water-pollinated, species rely on. The pollen grains are kept above the water, where they are transported via floating male flowers that plow into female flowers to effect pollination. Examples are *Enhalus*, *Lagarosiphon* and *Vallisneria*.

Darwin's and Cavolini's observations received only passing interest from other investigators, who continued to concentrate on animal and wind pollination. Only in the past two decades have botanists asked broader evolutionary questions about hydrophilous pollination. Are there general principles that apply to all hydrophilous pollination systems? What features should characterize efficient systems for pollination on a two-dimensional plane such as the surface of water? What shape and size should the pollen be? Should pollen be dispersed singly or in groups?

Such questions fall within the realm

of search theory, first developed during World War II by the mathematician Bernard O. Koopman and his colleagues at the Antisubmarine Warfare Operations Group of the U.S. Navy. In a simple but elegant derivation, Koopman showed that if a search vehicle traces a somewhat random path in two dimensions, its probability of encountering a fixed target rapidly increases with the width of the path it traces. (Mathematically, the relation is $p = 1 - e^{-wL/A}$, where p is the probability of hitting a target, e is the base of natural logarithms, w is the width of the path swept by the search vehicle, L is the length of the



POLLEN ON WATER'S SURFACE is a second method. To form pollen rafts, some species release filamentous or oval pollen; others have spherical pollen embedded in long tubes. Stigmas tend to be threadlike in marine species such as *Amphibolis* and *Halodule* and cuplike in freshwater ones such as *Ruppia* and *Lepilaena*.

path and A is the search area.) Koopman's equation had immediate military significance: even a modest increase in the range of a ship-borne radar dramatically increases the probability of detecting a fixed target during a random search.

Koopman's equation applies not only to ships but also to pollen grains in the hunt for stigmas. The equation makes it possible to set a lower bound on the search efficiency of pollen grains if the grains do not trace completely random paths. If the probability of encountering a target is low (a reasonable assumption in aquatic pollination), then a small increase in the size of the search vehicle will substantially heighten the probability of hitting a stigma lying on the surface.

The evolutionary significance of Koopman's equation is clear for *Vallisneria*, the plant studied by Erasmus Darwin. Here the floating male flowers sweep a path several thousand times wider than an individual pollen grain can, thus increasing search efficiency. A similar pollination system occurs in a different species: the African pondweed *Lagarosiphon*, studied by C.D.K. Cook of the University of Zurich. As in *Vallisneria*, male flowers are released underwater and float to the surface. There three sterile stamens become erect, functioning like miniature sails. The long, fertile stamens, which unfold parallel to the water's surface, bear sticky pollen at the end of the ramrodlike filaments. The male flowers link together in large rafts, colliding with the female flowers floating on the water.

But what about such plants as the one Cavolini studied, *Z. marina*, which releases its pollen directly onto the water's surface? Are the predictions of wide search paths likewise verified? To answer these questions, R. Bruce Knox of the University of Melbourne in Australia and I examined the pollination biology of several genera of hydrophilous plants in the South Pacific. One sea grass studied was *Halodule pinifolia*, which grows along sandy coasts in the Fiji Islands. While conducting fieldwork with P. B. Tomlinson of Harvard University and John A. West of the University of California at Berkeley, I found entire *Halodule* populations to be almost completely exposed during the low spring tides. Then, the white stamens of *Halodule* slowly release the floating long, noodlelike pollen onto the surface of the sea.

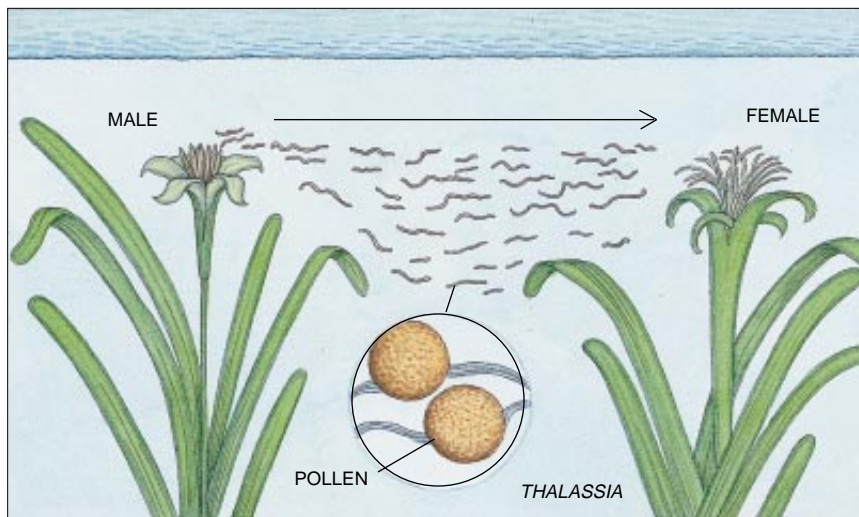
The pollen noodles have coatings of proteins and carbohydrates that make them sticky. They adhere to one another, forming rafts that resemble snowflakes. Millions of these floral search ve-

hicles are carried along as the tide returns to the shallow pools where the filamentous stigmas of the female plants float. The collision of the search vehicles with the stigmas on the water's surface results in pollination.

Many other sea-grass genera also assemble search vehicles that widen the search path, although the production varies slightly. In *Amphibolis* in Australia and *Thalassodendron* in Kenya, the male flowers float to the surface and there release filamentous pollen that assembles into latticelike rafts. Some unrelated sea-grass genera lack noodle-like pollen but compensate in other ways. In Fiji the small oval pollen grains of *Halophila ovalis* do not form rafts but are embedded inside sticky mucilaginous tubes that assemble into rafts, appearing as floating feathers. In Australia the freshwater species *Lepilaena cylindrocarpa* releases spherical pollen in floating mucilaginous mats that resemble tiny omelettes. These mats fall into depressions caused by the female flowers.

Thus, it is clear that many hydrophilous plants—*Vallisneria*, *Halodule*, *Halophila* and *Lepilaena*, among others—together represent an example of convergent evolution: unrelated species have evolved similar means (floating search vehicles) that serve to increase pollination efficiency. Of course, some hydrophilous species have unique adaptations, mechanisms that perhaps are indicative of evolutionary whimsy. What military strategist could fail to be intrigued by the horned pondweed *Zannichellia palustris*? Cook and I and our respective students You Hao Guo and Rebecca Sperry found *Zannichellia* to form ominous floating clouds that slowly drop round pollen grains onto the stigmas below. Fortunately, in this case, being hit by such a botanical depth charge results not in flower destruction but plant reproduction. And what golfer could fail to be delighted by the pollination system of another freshwater plant, *Hydrilla verticillata*, also studied by Cook? Here, male flowers float to the water surface and explosively catapult their pollen through the air to the floating female flowers. Because *Hydrilla* pollen is destroyed by contact with water, only the holes-in-one count. Given the vast amount of pollen released, the probability that a stigma is struck is actually fairly high.

So far I have discussed the pollination systems of plants whose pollen is transported above or on the surface of the water. In such cases, the pollen moves in two dimensions. Some species have pollination systems that



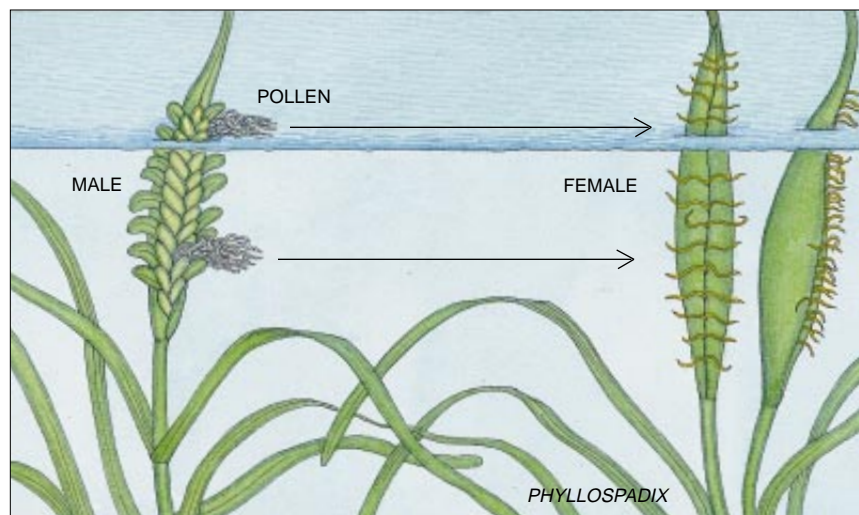
UNDERWATER POLLINATION is a third method of reproduction. In some species, filamentous pollen or pollen grains in mucilaginous strands are carried underwater by currents. In others, pollen denser than water is released. Examples include *Thalassia*, *Syringodium* and a species of the freshwater genus *Lepilaena*.

operate in three dimensions—that is, below the surface [see “Submarine Pollination,” by John Pettitt, Sophie Ducker and Bruce Knox; SCIENTIFIC AMERICAN, March 1981].

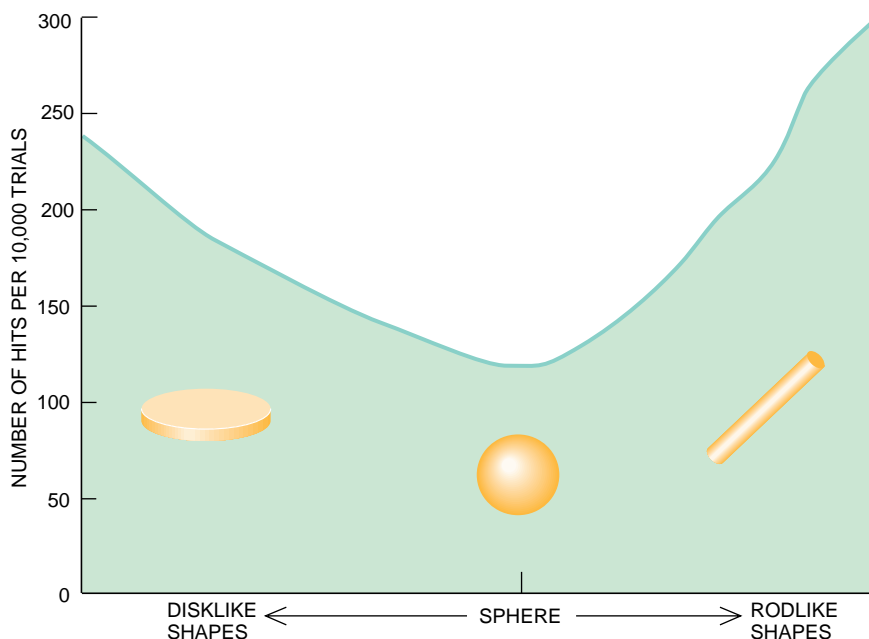
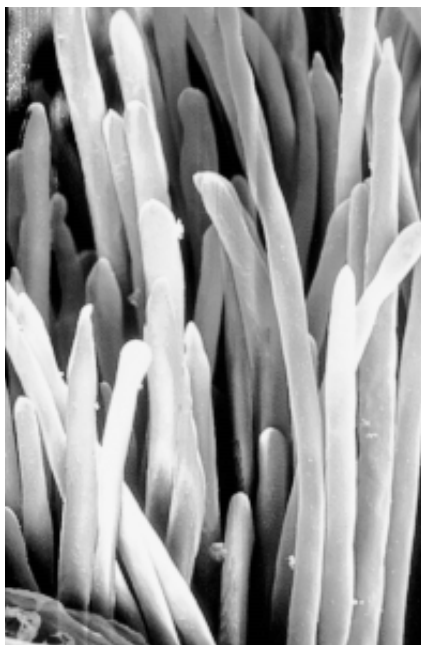
Pollination strategies in three dimensions seem to be less common than the two-dimensional varieties, probably because they are intrinsically less efficient. In three dimensions, pollen and stigmas are dispersed throughout a volume rather than concentrated on a single plane (such as the water's surface), and so more pollen is needed. The consequences of random motion also differ greatly in three dimensions. A ran-

dom hunt is far more efficient in two dimensions because the search path is recurrent: any stigma on the plane will eventually be hit given enough time. The same cannot be said for a three-dimensional search, even given an infinite amount of time [see “Brownian Motion and Potential Theory,” by R. Hersch and R. J. Griego; SCIENTIFIC AMERICAN, March 1969].

Three-dimensional pollination has tended to evolve in hydrophilous plants that ordinarily would have little opportunity to engage in two-dimensional pollination—that is, in plants that are always submerged. An example is the tur-



MIXED MODE of pollen transport, used by *Phyllospadix* and *Zostera*, combines surface with submarine pollination. Surface pollen tends to be slightly more filamentous than submarine pollen. Underwater delivery occurs in subtidal zones—that is, in populations that never reach the surface, even during low tide.



OPTIMAL POLLEN SHAPE for underwater pollination was determined by analysis on a supercomputer. Spheres were deformed into ellipses of equal volume, either as long rods

or as disks. The rods proved best at striking a target and compare well with actual submarine pollen grains, such as those of *Phyllospadix* (photograph).

tle grass *Thalassia testudinum*, a Caribbean plant that Tomlinson, Thomas Elmquist of Umeå University in Sweden and I studied on the island of St. Croix. *Thalassia* releases its round pollen underwater, embedded in elongated strands of mucilage. Having been driven underwater by waves, the strands collide there with the stiff, bristly stigmas of the female plants. A similar underwater pollination mechanism of embedding round pollen on long, mucilaginous strands is a feature of an unrelated freshwater species: *Lepilaena bilocularis*, found at Lake Ellesmere on South Island of New Zealand.

I wanted to see if this pearls-on-a-string approach by these geographically remote and taxonomically distant species represented an efficient three-dimensional strategy. Together with my mathematics students Tyler Jarvis, now at Princeton University, and Scott Cromar, now at Rutgers University, I ran a series of numerical experiments on a supercomputer at the IBM Scientific Computing Center in Palo Alto, Calif. We deformed spheres elliptically to varying degrees while keeping their volume constant, thus producing a variety of long strings or flattened Frisbee-like disks. We then determined how frequently each shape encountered randomly positioned targets. In our simulations we found that all the elliptical deformations were more efficient in three-dimensional searches than were the spheres [see illustration above].

Recently my student David Smith,

now at Princeton, David A. Olson, then at New York University's Courant Institute of Mathematical Sciences, and I confirmed these numerical experiments analytically. The equations also revealed something the supercomputer experiments had missed: shapes that are only slightly disklike are the least efficient at three-dimensional search. Still, the general conclusion holds. The search vehicles of *T. testudinum* in the Caribbean Ocean and *L. bilocularis* in New Zealand—each consisting of pollen attached to a mucilaginous strand—represent highly efficient solutions to the problems of locating objects scattered in three dimensions.

Some hydrophilous species mix both two- and three-dimensional strategies. For example, *Enhalus acoroides*, a sea grass I studied in the Indonesian island of Banda, flowers only during low spring tides. Like *Vallisneria*, the male flower buds float to the water's surface, open and are captured within the rumpled petals of the female flowers. As the tide rises, the petals of the female flowers close, trapping the male flowers within. But *Enhalus* disperses some pollen directly on the water's surface.

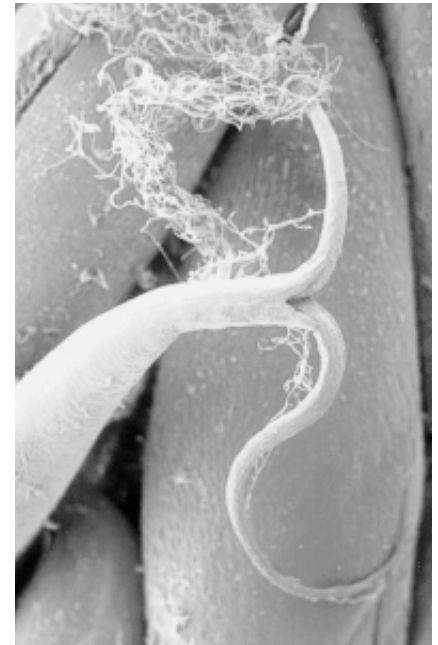
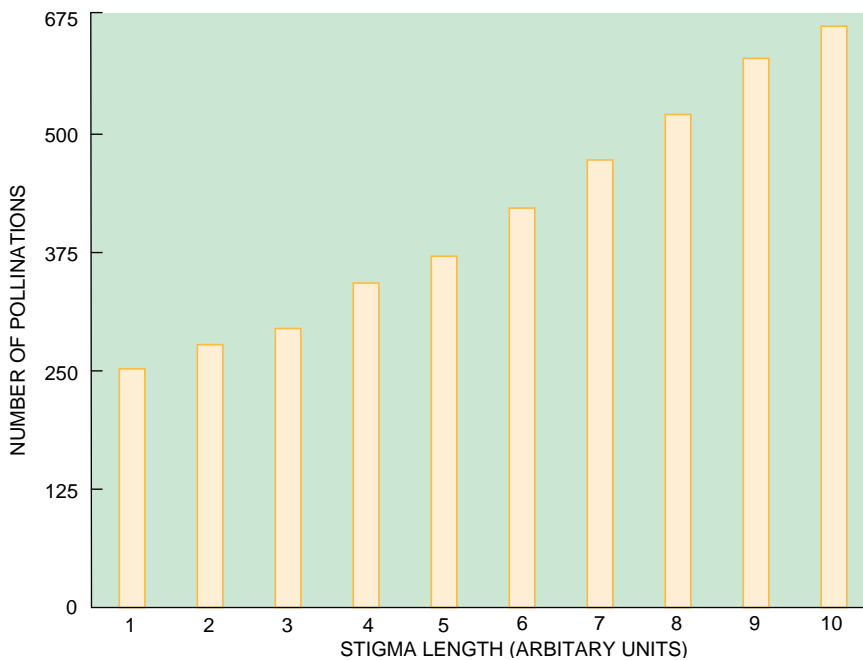
The surfgrass *Phyllospadix scouleri* also disperses noodlelike pollen both on and below the surface. Studying a population along the northern California coast, Tomlinson, my student Kevin Nieznanski and I observed floating pollen search vehicles of *Phyllospadix* collide with female stigmas. But electron micrographs of stigmas collected far

below the water's surface also revealed pollen, indicating that submarine pollination can take place.

Yet another example of mixed surface and submarine pollination occurs in the plant originally studied by Cavolini: *Z. marina*. A.W.A.M. de Cock of Catholic University in the Netherlands found that although *Zostera* pollen released underwater in aquariums slowly sinks, pollen dispersed at low tide in intertidal populations floats on the surface. Roger H. Laushman of Oberlin College, Mary H. Ruckelshaus of the University of Washington and I, working at Friday Harbor Marine Laboratories in the San Juan Islands, off Washington State, confirmed de Cock's report. We found that pollen rafts resembling snowflakes float on the surface; however, we also observed linear bundles of noodle-shaped pollen dispersed beneath the surface of the sea.

Efficient search methods are not the only way to increase the chances of pollination. Evolution can also select for stigmas that can readily be found. Unfortunately, the design of targets that could easily be hit was not considered a high-priority task by the military strategists who developed search theory. So, much of the analysis of target design has fallen to botanists.

From the stigma's point of view, there are at least two possible ways to heighten the chances of being struck by a pollen grain or pollen raft. First,



OPTIMAL STIGMA SHAPE in surface pollination was determined by deforming spheres into increasingly longer ellipses. Pollen grains collided with the long, elliptical stigmas more

frequently than they did with the round stigmas. The results compare favorably with stigmas of real plants, such as that of *Zostera marina* (photograph, with pollen strands clinging).

the effective area of the target can be broadened. Second, the stigma's shape can be altered to increase the probability of encounter.

The floral structures of many water-pollinated plants embody the first solution. Some blossoms, such as those of *Vallisneria* and *Enhalus*, create depressions in the water's surface, forming a target area much larger than a stigma or even an entire female flower. Another example is provided by *Lepilaena cylindrocarpa* in Australia. Usher Posluszny of the University of Guelph pointed out to me a small bract that holds three separate stigmas together before fertilization. Thus united, the three stigmas of the female flower, each resembling a baseball mitt, cause a dip in the surface of the water.

The oscillatory motion of some plant parts can also enlarge the effective target area. In a slow-moving stream, the elongated stalk of *Ruppia marina* functions much like a windshield wiper: it causes the flowers to sweep gently back and forth, collecting the snowflake-shaped pollen rafts. Floral structures may also have localized effects. Joseph D. Ackerman, then at Cornell University, observed how submerged flower clusters of *Zostera* affect underwater flow patterns. He found that under laboratory conditions the altered flow can concentrate pollen near the stigmas.

Investigation into the second possible means of increasing target efficiency—changing target shapes—has begun only in the past few years. In a series of su-

percomputer simulations, James A. Sethian of Berkeley and I found that in two dimensions, filamentous stigmas are far more likely to be hit than are circular stigmas. The extremely long, thread-like stigmas of the sea-grass genera *Halodule*, *Halophila* and *Thalassodendron* seem to confirm the prediction [see illustration above].

Field observations also contradict the assumptions made by some previous workers, who thought that hydrophilous plants rarely flower or pollinate. I have found that flowering and cross-pollination (the transfer of pollen from one individual plant to another) to be common, though sometimes ephemeral, events. The frequency of flowering—and by implication cross-fertilization—can directly affect genetic diversity of the populations. By using a technique called starch-gel electrophoresis, Laushman has found cross-pollination in *Zostera* populations to be relatively frequent, particularly in the intertidal area where surface pollination happens.

Yet other investigators find little diversity. Based on his studies of the freshwater species *Ceratophyllum demersum*, Donald H. Les of the University of Wisconsin at Milwaukee believes hydrophilous plants may in large part be genetically uniform. Such uniformity could arise from self-pollination. For instance, C. Thomas Philbrick of Rancho Santa Ana Botanic Garden in Claremont, Calif., has found that in a submerged species of *Potamogeton*, minute air bubbles can carry pollen from the

anther to the stigma of the same flower. Genetic homogeneity could also result from infrequent flowering and large clone sizes in a population.

Although the mechanics of water pollination has not been able to detail the genetics of hydrophilous populations, it does offer clues to explain why such plants followed an evolutionary path different from their terrestrial counterparts. The noodlelike shape of the pollen is one distinctive feature of hydrophilous plants. To study the emergence of such pollen, C. J. Humphries of the London Natural History Museum and I have attempted to reconstruct the family tree of the sea-grass family Cymodoceaceae. We found that this family, which includes *Thalassodendron*, *Amphibolis*, *Syringodium*, *Halodule* and *Cymodocea*, shares a common ancestor with *Posidonia* (a sea grass found in the Mediterranean and Western Australia) and Zosteraceae, a family that encompasses *Zostera*, *Phyllospadix* and the Australian genus *Heterozostera*. Our analysis suggests that this common ancestor had noodle-shaped pollen. Thus, noodlelike pollen probably evolved only once, explaining why other unrelated sea-grass genera such as *Halophila*, *Thalassia* and *Enhalus* still retain round pollen similar to that of terrestrial plants.

Yet another striking feature of hydrophilous plants has to do with dioecism—the separation of male and female flowers into distinct plants. More



BREACHING THE WATER'S SURFACE during the spring low tides is the only time many marine hydrophilous plants, such as a population of *Phyllospadix* along the coast of Mon-



terey, Calif. (left), have to release pollen or flowers on the surface. The pollen of many such hydrophilous species assemble into rafts, such as those of *Amphibolis* (right).

than half of all hydrophilous species are dioecious. In contrast, only about 3 or 4 percent of terrestrial species are dioecious. Dioecism in hydrophilous plants might have evolved because of the physical incompatibility between the mechanisms of waterborne pollen dispersal and pollen capture within a single flower. A combined floral morphology would likely result in a flower capturing its own pollen before release, defeating the ability of the plants to cross-fertilize.

Another possible reason for the observed high rate of dioecism is that it helps to prevent inbreeding. Because many hydrophilous populations consist of large clones, inbreeding can result if male and female parts occur on the same plant. Alternative mechanisms of outbreeding typical of terrestrial plants probably would not function as well in hydrophilous plants. For example, the maturation of male and female flowers at different times, a phenomenon typical in land plants, would probably be difficult to synchronize in a large sea-grass clone.

The unusual features of hydrophilous plants render them not only fascinating but also extremely useful as study organisms for many problems in the evolutionary ecology and demography of plants. The life span of hydrophilous pollen is easy to determine because the pollen grains of many hydrophilous plants display cytoplasmic streaming. This feature, readily observed under a microscope, is simply the movement of

cytoplasm within the pollen grain. I found that *Zostera* pollen, for example, has a strikingly short lifetime: almost all the pollen dies within eight hours after release. In contrast, determining the life span of terrestrial pollen is much more difficult: terrestrial pollen generally must be stained to determine viability.

Furthermore, the fate of individual pollen grains of surface-pollinated species is easily determined. One can simply examine, frame by frame, videotapes of the water surface and trace the paths of the grains. This approach is clearly impractical with plants whose pollen is carried by wind or animals.

Hydrophilous species may yield insights into patterns of geographic colonization and the genetics of plant populations because the populations of freshwater hydrophilous plants are in essence reproductively isolated. Waterborne pollen cannot move between ponds. Gene flow between populations must therefore transpire primarily by transfer of fruits or small vegetative pieces that break away. Vigorous clonal growth in most water-pollinated plants also makes them ideal for ecological experiments: one can expose the same genotype to many different environments.

Compared with the widespread interest in wind and animal pollination, little work has been done on hydrophilous pollination since Cavolini first discovered *Zostera* flowers in the Bay of Naples. Although water-pollinated

plants do not produce large, showy flowers, as do many terrestrial plants, I find them to be exquisitely beautiful. The plants provide opportunities for both amateur and professional botanists to make original observations in natural history and to study more closely convergent evolution in aquatic environments.

FURTHER READING

- SEARCH AND SCREENING. B. O. Koopman. Pergamon Press, 1980.
- HYDROPHILOUS POLLINATION. P. A. Cox in *Annual Review of Ecology and Systematics*, Vol. 19, pages 261-280; 1988.
- TWO-DIMENSIONAL POLLINATION IN HYDROPHILOUS PLANTS: CONVERGENT EVOLUTION IN THE GENERA HALODULE (CYMODOCEACEAE), HALOPHILA (HYDROCHARITACEAE), RUPPIA (RUPPIACEAE), AND LEPILAENA (ZANNICHELLIACEAE). P. A. Cox and R. B. Knox in *American Journal of Botany*, Vol. 76, No. 2, pages 164-175; February 1989.
- SURFACE AND SUBMARINE POLLINATION IN THE SEAGRASS *ZOSTERA MARINA* L. Paul A. Cox, Roger H. Laushman and Mary H. Ruckelshaus in *Botanical Journal of the Linnean Society*, Vol. 109, No. 2, pages 281-291; June 1991.
- UNDERWATER POLLINATION, THREE-DIMENSIONAL SEARCH, AND POLLEN MORPHOLOGY: PREDICTIONS FROM A SUPER-COMPUTER ANALYSIS. P. A. Cox, S. Cromar and T. Jarvis in *Pollen and Spores: Patterns of Diversification*. Edited by S. Blackmore and S. H. Barnes. Oxford University Press, 1992.