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Plants in Heat

In spring snow, skunk cabbages are warm islands where seeds form and some creatures spawn early

by Roger M. Knutson

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In 1672, John Josselyn, Gent., in a book of "New England Rarities," natural phenomena he claimed to have discovered, offered probably the first written description—a somewhat inadequate one—of the skunk cabbage, or skunkweed (*Symplocarpus foetidus*), of eastern North America.

> This plant is one of the first that springs up, after white hellebore, in the like wet and black grounds, commonly by hellebore; with a sheath, or hood, like dragons; but the pestle is of another shape; that is, having a round purple ball on the top of it, beset (as it were) with burs. . . . The whole plant sents [*sic*] as strong as a fox. It continues till August.

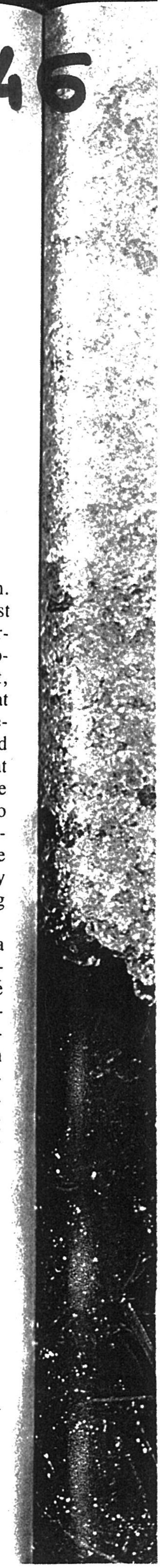
Skunk cabbage is so common over most of its geographical range that some of its fascinating but less obvious characteristics might be overlooked today as they were 300 years ago by Gentleman Josselyn. A plant that produces flowers that melt their way through early spring snow and ice, that maintains its flower temperature at a nearly constant 72°F—as much as sixty-three degrees higher than surrounding soil and air—that annually pulls itself deeper into the ground by contracting its roots, and that provides centrally heated housing for several sorts of small creatures deserves more than a reputation for a bad smell.

Eastern skunk cabbage is one of a few temperate-zone representatives of a large family of plants, the Araceae, or aroids. Only eight aroid genera occur in the United States; five are represented by a single species. Some of the mostly tropical relatives of *Symplocarpus* may help reveal the source of some of its unique properties. The aroids include arums, caladiums, callas, dieffenbachias, philodendrons, anthuriums, and other, mostly tropical house and garden plants. In the leaf, stem, and root cells of all aroids, sharply pointed microscopic crystals of calcium oxalate give most parts of the plants an extremely peppery taste and will inflame the mouth tissues of any hapless animal that chews the plants. Even if boiled in several changes of water, skunk cabbage leaves may bite the tongue that eats them. *Dieffenbachia* is sometimes called dumb cane because it can temporarily reduce or eliminate speech in anyone unfortunte enough to chew some of the fresh plant.

Another uncommon feature of all members of the family Araceae is an unusual flower structure, or more precisely, an inflorescence. The short, thick stem that bears the flowers is called the spadix. The spadix is usually large and complex, but it may be a simple ball of tightly packed fleshy flowers, the pestle that Josselyn referred to. The whole flower cluster, as well as the flowerless appendage present in some aroids, is at least partly surrounded by a leaflike spathe, often deeply colored and attractive to potential pollinators. Both spathe and spadix tend to be yellow or brownish purple, like plants pollinated by carrion flies or beetles. Some tropical aroids have massive spathes and spadices. An early twentieth-century photograph of an aging Hugo de Vries shows the Dutch botanist-geneticist overshadowed by the spathe and spadix of *Amorphophallus titanum*, a Sumatran plant, whose inflorescence approaches six feet in height and three feet in width.

Lamarck seems to have been the first to report, in 1778, that during flowering, the spadix of some aroids produced detectable amounts of heat, much like the elevated temperature that accompanies a mammal's estrous period. In blooming *Arum italicum* and *A. maculatum*, Lamarck found heat production was centered in the sterile appendage, reportedly thirteen to eighteen degrees warmer than the surrounding air. Josselyn, who may have only observed plants collected by others, did not notice that the flowering skunk cabbage also produces heat.

By 1822, Nicolas de Saussure, a Swiss botanist best known for his research on photosynthesis, linked the heat production in the spadix of *A. italicum* with a rapid rate of oxygen absorption. Living tissue uses oxygen in the process of respiration, and Saussure had measured a high rate of respiration in the *Arum* spadix during flowering. All living organisms, plant and animal, respire and produce some heat, but very few plants or parts of plants respire rapidly enough or are large enough to be measurably warmer than their surroundings. Interestingly, more recent investigations of the



In early spring, the skunk cabbage's only visible part is the purple green spathe, and as soon as it appears, the spadix inside begins to heat, melting surrounding snow and ice.

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Later in spring, after skunk cabbage has completed its flowering and attendant heating process, its huge leaves, initially rolled-up cigar shapes, begin to unfurl.

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biochemical details of respiration in a number of aroids, including skunk cabbage, have shown that cyanide, carbon monoxide, and several other substances poisonous to most oxygen-using organisms have little or no effect on the very rapid respiration of aroids.

While a few aroids do not seem to heat up at all, most do have a short period of rapid respiration and heat production centered in the spadix. Where present, the heating is coincident with maturation of the plant's pollen and egg cells. Some aroids time pollination activity with considerable precision by producing volatile chemicals that are pumped into the environment by the pulse of heat generation. Many aroids seem to be olfactory mimics of excreta or decaying flesh, producing odoriferous volatile chemicals with names such as skatole or cadaverine. These powerful scents advertise the enclosed spaces inside the spathe and lure potential pollinators with promises of warmth, food, and places to lay eggs.

Residents and temporary tenants in various aroids include the so-called arum frog, which lives in the spathe of the South African pig lily (*Zantedeschia*) and feeds on the frequent insect visitors or on spiders that also wait for insect prey. Creatures that look for food or warmth in the complicated spathe of a heated *Arum* flower may well find themselves forced to stay longer than they had planned or even providing food for predatory residents. To attract pollinating insects, the tropical *Amorphophallus* releases fetid odors and provides specialized dispensable nutritious cells on the surface of the spadix. This food supply may help to assure that insects attracted by odors will remain with the plant long enough to increase chances of effective pollination.

As the few temperate-zone aroids moved out of the tropics into less equable climates, natural selection modified details of their flowering, heating, and animal attraction. For the past seven years, I have followed the life of skunk cabbage in northeast Iowa, at the extreme western limit of the plant's geographical range in North America. (Western skunk cabbage, *Lysichiton americanum,* found in Washington and Oregon, is a quite different plant.) Eastern skunk cabbage's North American distribution corresponds to the eastern deciduous forest, where the plant finds the deep, black, mucky soil it requires. The plant seldom grows alone; in summer, the enormous green leaves of a skunk cabbage patch have a tropical luxuriance. On its northward odyssey, the plant seems to have retained elephant-ear-sized leaves, like those of *Caladium.* Individual plants of *Symplocarpus foetidus* vary remarkably little over their range in North America. Their dark, heavy, marble-sized seeds usually germinate within a few feet of the parent plant. Squirrels or other rodents occasionally store seeds, accounting for local dispersal, but the specific mechanisms of skunk cabbage's long-range dispersal remain something of a mystery. Present populations may be the remains of a much wider ancient distribution. Like many plants native to eastern North America, *Symplocarpus* is also found in Japan and along the eastern edge of the Asian mainland.

I began to study skunk cabbage during a February 1971 visit to the forested edge of a frozen marsh, which was fed by small seeps of water from the limestone and shale layers that outcrop along hillsides in the driftless area of extreme northeast Iowa. Although the temperature was in the twenties, the soil in such places seldom freezes

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more than a few inches deep, which may explain why several purple green spathes, or hoods ("like dragons," Josselyn said), protruded through the frozen crust at the wooded edge of the marsh. A melted circle in the snow and ice surrounded each hood. The spathe of the skunk cabbage has some of the color of its tropical relatives, but it is much thicker. Spathe tissue consists almost entirely of small separated air spaces, resembling fine styrofoam, which effectively insulate the spadix. Inside the hood, each spadix was warm to my touch.

The next day, I returned with a thermistor thermometer and made the first of many measurements of the internal temperature of those overheated flowers. I found that heating was most intense during the early stages of blooming, after the stigmas were exposed and receptive but before the pollen was released. For two weeks or more, an individual spadix could maintain a temperature thirty-six to sixty-three degrees above air temperature, an impressive extension of the heating capability of the tropical aroids and the temperate-zone *Arum,* which heat for only a few hours or at most for parts of several consecutive days. Because of the skunk cabbage's extended period of heat production, flowering and seed production have a much earlier start. I found that flowers heated for two weeks or slightly longer and then died when air and soil temperatures stayed below freezing. New spathes continued to emerge well into April, however, and every year some of them were accurately timed to begin seed production as early as possible. Hence, the plants would seem to provide their own tropical climate for early embryo development.

Although the intensity and duration of heating were impressive, my early temperature measurements also revealed that the enclosed and insulated spadices of the skunk cabbage remained at nearly the same temperature regardless of the temperature of surrounding air and soil. On colder days or as the air cools during the night, the spadix should lose heat more rapidly; but since it maintains a constant temperature, it must generate more heat as air temperatures fall. The plants seem to have not only a furnace but a thermostat as well.

As Saussure demonstrated with *A. maculatum,* heating is tied to oxygen use or to the respiration process that uses oxygen. My skunk cabbages seemed to respire more rapidly at low temperatures than at high temperatures, a most unplantlike thing to do. On warm March days, I could measure the rate of oxygen use in the blooming flowers by sealing a small pickle jar—christened the Heinz-Vlasic respirometer—over the spathe and spadix and then monitoring pressure changes inside the jar. I monitored oxygen use with my improvised respirometer exposed to warmish March air, and again with the instrument packed in snow, which lay in unmelted piles under trees at the marsh edge. When the temperature around the spathe dropped from 63° to 45°, the spadix nearly doubled its use of oxygen. Repeated observations on days with different air temperatures provided sound evidence that in this one regard my plants were behaving more like skunks than cabbages.

The absolute rate of oxygen use measured at cooler temperatures was in itself surprising. Generally, among homoiothermal, or warmblooded, animals, the smaller the animal, the faster its rate of respiration. The relationship reflects a relatively simple physical principle: in a smaller animal the ratio of surface area to volume is higher,

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As soon as the spathe emerges aboveground or out of water left by melting snow, it opens in a pointed ellipse, exposing the spadix and drawing pollinators and mating creatures to its warmth.

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with more surface radiating heat for each unit of volume generating it. The respiration rate of skunk cabbage spadices is approximately that of warm-blooded animals of equivalent weight. If spadices of different weights are compared, smaller ones have a more rapid rate of respiration than larger ones at the same temperature. At air temperatures near freezing, a seemingly inactive skunk cabbage spadix is using oxygen and burning food at a rate nearly equal to that of a small shrew or a hummingbird.

Constant day and night monitoring of air and spadix temperatures showed that skunk cabbage plants have a limited capacity to generate heat. Whenever air temperatures dropped below freezing, a slow process of cooling began, and if air temperatures remained below freezing for more than twenty-four hours, the flowers would often die. As long as air temperature stayed above freezing, the spadix temperature stayed at a nearly constant 72° to 74°.

The spadix's response to sudden, unnatural cooling helps us to understand the mechanism that adjusts the skunk cabbage's rate of respiration. If the whole spathe is packed in snow or crushed ice, the temperature of the spadix drops quickly and continues to fall for almost one hour. It then begins to slowly rise to its former level. The constant response time of one hour strongly suggests that movement of some internal substance controls the rate of respiration. The spathe may communicate the drop in external temperature to the spadix by means of a hormonelike chemical, whose identity and working mechanism are still unclear. The hormonal substances that usually control plant activities have no effect on the rate of heat production in the skunk cabbage.

The tiny island of dependable, near-tropical warmth inside the spathe of the blooming skunk cabbage draws a variety of early spring insects and other invertebrates, but most are probably casual visitors. A few may have more important relationships with the plant, based on its ability to continue heating for many days. Ordinarily, honeybees do not fly well if air temperature is below 65°, but they have been observed visiting skunk cabbage at air temperatures as low as 42°. During their stay in the spathe, the bees seem to accumulate enough energy to reach the next plant or their hive. In March, with air temperatures below 50°, I have watched bees collecting pollen from pussy willow catkins and skunk cabbage at the same location. Temperatures inside spathes in the sun were near 80°. Skunk cabbage may attract bees by scent as well as warmth. Bees do not ordinarily visit flowers having the smells associated with most aroids. But to insects—and to humans—an uninjured skunk cabbage flower has a faintly sweetish smell that gives no hint of the mephitic odor produced by any damaged part of the plant—a scent that one observer described as a mixture of skunk, putrid meat, and garlic.

Spiders are frequently found in skunk cabbage spathes, presumably waiting for visiting insects, but at least one kind of spider may be using the spathes for another purpose. In mid-April on Beaver Island in northern Lake Michigan, where nearly a foot of snow had yet to melt in the shady cedar swamps favored by skunk cabbage, I examined one hundred fifty flowering plants and found forty occupied by one or more individuals of the same species of spider, *Pachygnatha brevis*. One of the so-called long-jawed spiders, this arachnid favors swampy areas, where because of its poor eyesight, it uses

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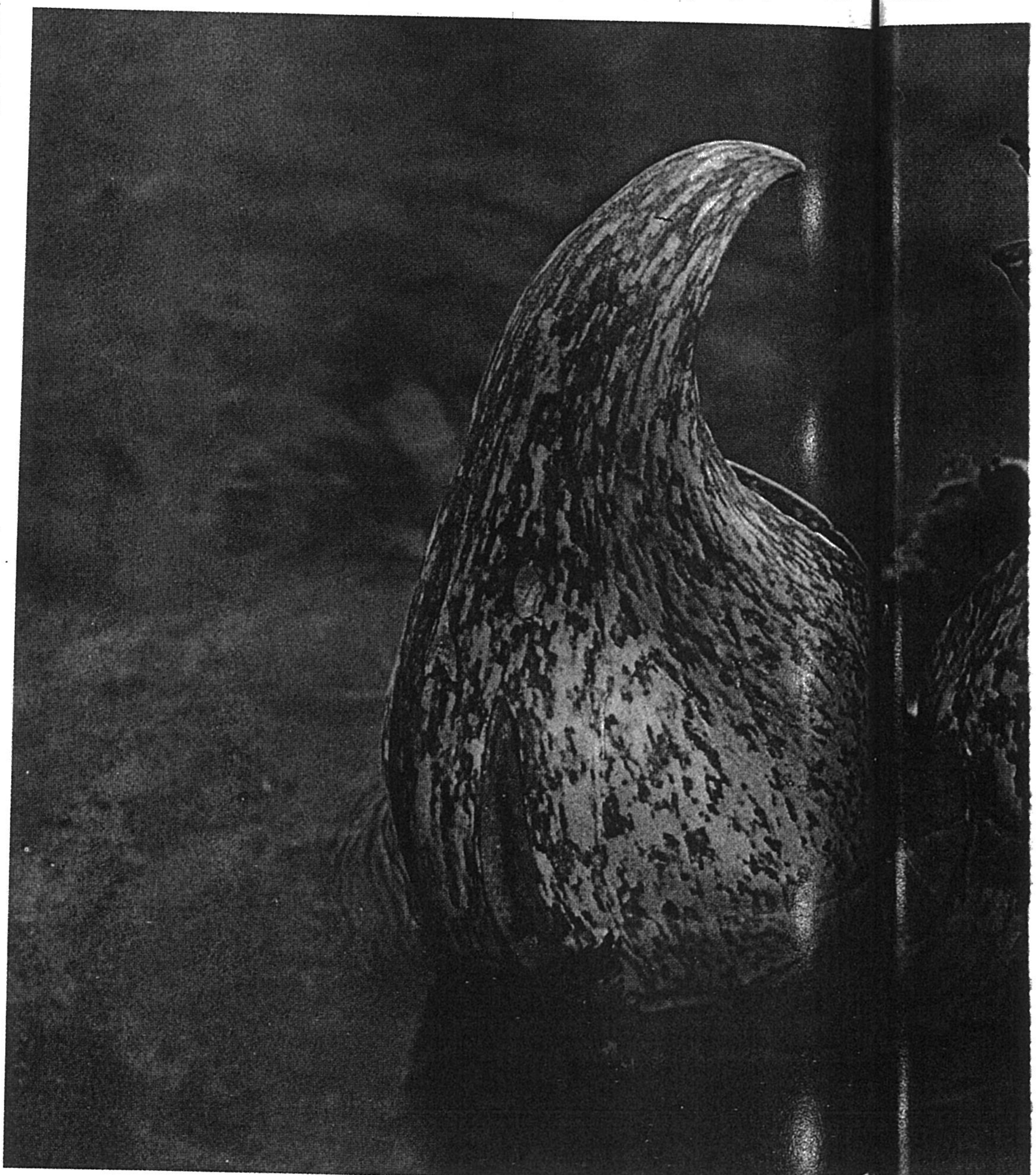


The spathe encloses the yellow or purple spadix, source of the plant's heat. The warmth and the sweetish scent given off by an undamaged spadix attract pollinators, such as bees.

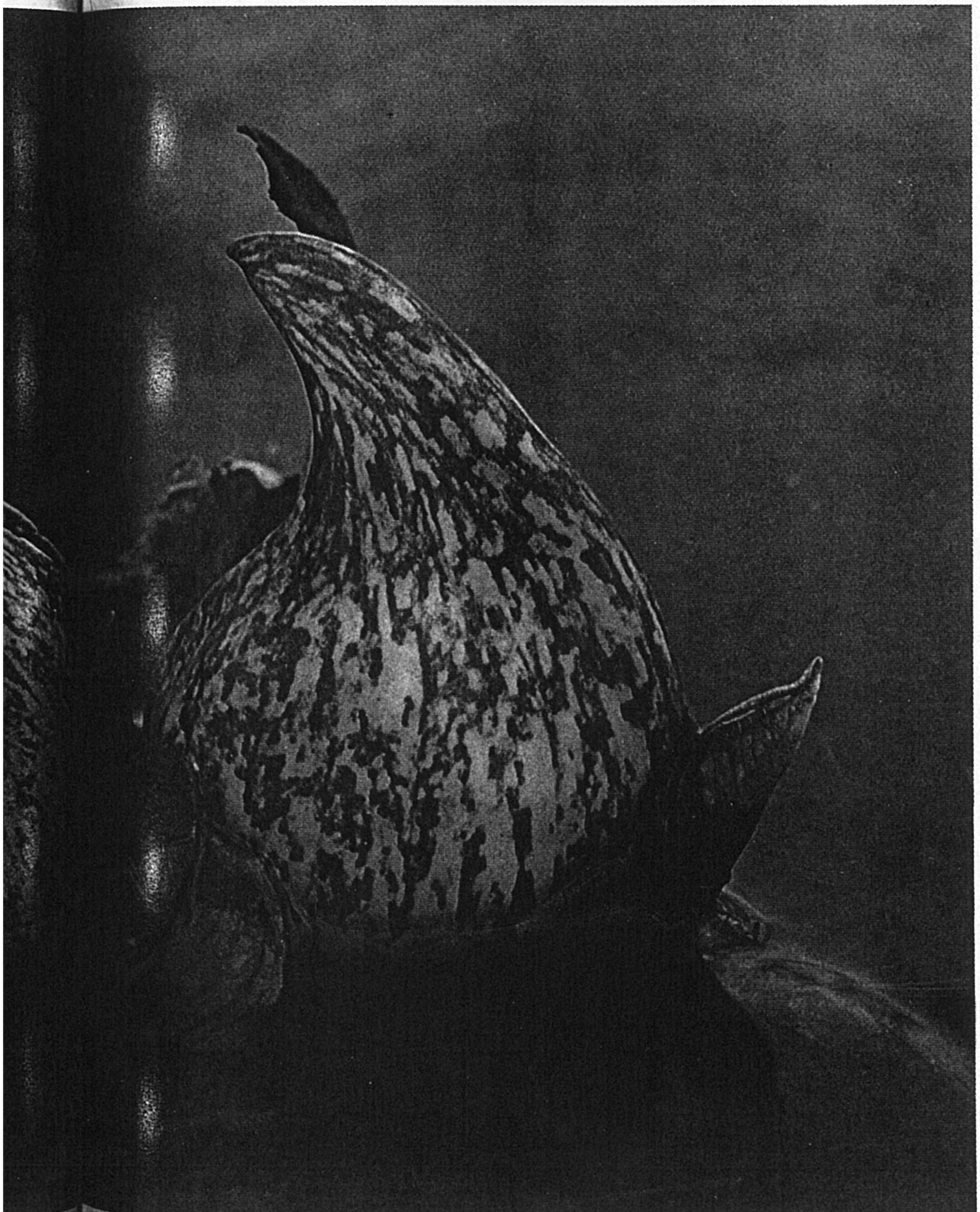
touch to find mates among the roots of semiaquatic vegetation. On Beaver Island, each spider had taken up a clearly visible position on the surface of a spadix. The spiders probably do not spin webs, indeed, no webs were present.

None of the spiders in the spathes had any insects, dead or alive. Four spathes held a pair of spiders, one male and one female. I suspect that in heated skunk cabbage spathes, *P. brevis* find convenient, centrally heated trysting places suitable for conceiving and hatching the next generation earlier than usual in the spring season. Every flower housing one or more spiders was in its earliest stages, having only stigmas exposed and no pollen. I examined an equal number of spadices in later stages of blooming, when the anthers have matured and pollen is being shed. These more mature spadices contained some insects and a few small harvestmen, but not one spider of either sex. If the spiders came to those heated chambers simply in search of prey, they would have found greater rewards later when abundant pollen was available.

The first time I dug a mature skunk cabbage plant from the ground in an attempt to move it indoors for easier control of its environmental temperature, I vowed I would not try again without power equipment. A large plant has a massive subterranean stem that may be a foot long and several inches in diameter. The plant's root is actually a severely shortened stem that annually pushes from six to eight leaves and usually two inflorescences above the ground. The lower end of the stem does not taper to a graceful point like the root of a parsnip, but has a broken to slightly rounded surface that appears to have been ground smooth. The hundreds of pencil-sized roots that extend almost horizontally for a foot or more from the stem have deeply ridged and wrinkled surfaces. These wrinkles and ridges explain the appearance of the lower end of the stem. Each year's roots grow out and down from the upper end of the stem, anchor themselves as firmly as possible in the mucky soil, and shorten in unison, wrinkling their surfaces and pulling the large stem into the ground a distance roughly equal to the stem's annual lengthwise growth. In the stem's forcible downward passage through the abrasive soil, the lower end, the oldest part, is smoothed. Gradually it dies and softens, making the polishing easier. The pebblelike seeds generally germinate on the surface of the soil. But within two or three years, the action of the young plants' contractile roots will pull them well below the surface. The subterranean stem may grow only a few millimeters (⅛ inch) or less per year, and most plants must grow five to seven or more years before they are large enough to produce the first spathe and flowers.

A large, mature skunk cabbage does not arouse the awesome sense of eternity that a giant redwood or ancient juniper inspires, but the skunk cabbage could conceivably be older. Unless their habitat is severely disturbed, individual plants of eastern skunk cabbage could probably live indefinitely. In the elaborate language of J. Marion Shull (*Journal of Heredity,* 1924), "Thus it happens that the skunk cabbage that is seen today growing in unpretentiousness in any bog may possibly outrival the sturdiest of oaks in point of age, may not improbably have occupied that very spot long years before Columbus set foot upon our shores and may continue there a thousand years and more from now if only the fates be kind."

After seven years of study, I see the eastern skunk cabbage as considerably more than the fox-scented plant Josselyn described in 1672. It has taken its tropical heritage northward, converting a mechanism for attracting specific pollinators at a particular time into a means of early blooming. The eastern skunk cabbage, a near-tropical plant, has become firmly and centrally placed in the web of the late winter life of North America. □



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