THE POLLINATION OF VALLISNERIA SPIRALIS

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(WITH PLATE IX AND SIX FIGURES)

Vallisneria has long been counted one of the classic examples of cross-pollination. Living vegetatively as a submersed aquatic, its dioecious flowers are brought together at the surface of the water in most ingenious fashion. These highly specialized flowers present the strongest contrasts, not only in size and structure, but in behavior as well, and give this plant its rank as one of the climax types with respect to floral differentiation. Specializations of such evident advantage for cross-pollination in a form so admirably situated for vegetative propagation seem to emphasize the importance of sexuality, or at least of seed production, in the higher plants.

While the general method of pollination in *Vallisneria* is well known, many interesting facts seem never to have been published, and the underlying principle has not been emphasized. The figures current in textbooks are highly generalized, and some of them are far from accurate. The story which they are intended to illustrate is likewise incomplete or in some cases highly distorted. In any event, neither figure nor story has done justice to the intimate history of pollen transfer in this remarkable plant.

It will be noted at once that the following account diverges radically from that suggested by KERNER'S (1) beautiful and widely copied figure. A comparison shows that these differences relate not only to the size and structure of the flowers, but are even more fundamental in character. KERNER emphasizes the fact that pollination is brought about through the contact of flowers floating on a level water surface; there follows an outline of a method of pollen transfer through the special agency of the surface film of water. The general drawing (pl. IX) is based on photographs of living flowers, measurements, and camera drawings of parts.

The epigynous seed-bearing flowers of *Vallisneria* are borne singly, each within its spathe at the end of a long scape, sometimes over a meter in length, which anchors the floating flower to the short upright stem at the bottom of the pond. Upon reaching the surface of the water through the elongation of this axis, the spathe opens at its outer end, but remains as a partial investment of the ovary until the seeds are nearly mature. The 3 spoonlike sepals soon separate, disclosing the 3 bifid stigmas which are coiled in the center of the flower (pl. IX). These fleshy stigmas are densely clothed with the stigmatic hairs, and their snowy whiteness constitutes the most conspicuous part of the flower. Rudimentary petals and slender staminodia are present, but as they seem functionless their discussion may be deferred to a subsequent paper.

The anchoring scape usually elongates sufficiently to permit the opening flower to assume an inclined position in the water as it is carried to one side by wind or current. The ovary, which is 20–25 mm. long before fertilization, is usually straight until the flower opens and has taken its position at the surface; later it often curves considerably in response to gravity, thus bringing the floral parts more nearly parallel with the surface of the water. This bending of the ovary at this stage is quite marked in plants growing in aquaria where the flowers are left undisturbed for some time.

The exposed floral parts are waxy and consequently are not wetted by the water, with the result that the flower comes to rest with a portion of its weight resting on the sepals and margins of stigmas supported by the surface film. This produces a slight depression of the water about the flower, perhaps 15 mm. in diameter, which is abruptly declined at its inner margin next to the pistillate flower. This sloping surface film plays an important part in capturing the floating staminate flowers, and later is intimately bound up with the actual transfer of pollen to the stigmas. Too much emphasis cannot be laid on the complete dependence of this plant upon the surface film of water for its pollination processes.

The staminate flowers are borne crowded numerously within the globose spathe which remains short-stalked at the bottom of the pond. A count of several of these flower masses showed an average of over 2000 flowers packed within each spathe, the whole group the homologue of the single pistillate flower which is solitary within its spathe. The staminate inflorescence resembles a large fern sorus surrounded by an indusium. This similarity is carried further by the striking resemblance of the slender-stalked unopen staminate flowers to polypod fern sporangia. Massed within the spathe these flowers are joined to the axis by slender pedicels of varying length, so as to completely fill the space between the stem and the spathe.

The pollen-bearing flowers are very tiny, less than 1 mm. in diameter before opening, and are simple in structure. The floral parts consist of 3 sepals, 2 functional stamens, and rudiments of petals. The sepals are of unequal size and are not symmetrically disposed; 2 are similar and stand nearly opposite; while the third and smaller one is placed laterally between them. This reduced sepal is the first to open. Numerous tapering and curved hairs cover the region about the base of the stamens and are doubtless of some importance, although their functions are not clear. The 2 stamens stand close together and have their parallel filaments united up to a point near the anthers (pl. IX).

At maturity the tip of the spathe opens slightly and the staminate flowers begin detaching from their slender stalks. The uppermost are the first to be shed, and 2 or 3 days may be necessary to empty a single spathe. These detached flowers rise slowly through the water to the surface and there very slowly open. In this respect *Vallisneria* stands in sharp contrast to the writer's (2) observations on *Elodea canadensis*. In that form the staminate flowers upon release dart to the surface and there fairly explode, scattering their pollen on the surface of the water. In *Elodea*, however, it is the free floating pollen that functions, while in *Vallisneria* the pollen retained in the anthers has the better chance of reaching the stigmas. SVEDELIUS (3) reports that the sepals of the detached staminate flowers of *Enalus acoroides* snap back upon reaching the surface of the water, although the pollen is retained in the anthers. In *Elodea canadensis*, and perhaps in *Enalus*, the snap of the sepals seems to be due in part at least to the release of gases imprisoned between the floral parts under water. The writer (4) has noted elsewhere that in *Elodea ioensis*, which has a long-stalked staminate flower, a bubble of gas is generally associated with the partly opened sepals, giving extra buoyancy to the submerged flowers, which tug at their anchorage like captive balloons.

No prolonged observations were made on the possible periodicity in the release of the staminate flowers of *Vallisneria*, although doubtless there is a relation between their detachment and the gases given off by the plant during times of brighter illumination. On one occasion it was observed that as the sun came up from behind a building and its direct rays fell on the spathe of the staminate inflorescence the rate of detachment was considerably increased for a time. In *Elodea canadensis* (2) there is a correlation between the coming of strong light in the morning and the rate of detachment of the staminate flowers. SVEDELIUS reports that the staminate flowers of *Enalus acoroides* are released mainly (if not exclusively) at periods of low tide. This habit is of peculiar significance from the fact that at high tide the pistillate flowers of that plant are wholly submerged and pollination would be impossible. No explanation of this relation was suggested in the paper.

The sepals of the staminate flower of *Vallisneria* completely invest the stamens until some time after the flower reaches the surface. They then slowly recurve, the smaller one being first to open (pl. IX), and as it touches the water it seems to function in orienting the flower so that when the pair of lateral sepals open there are formed 3 boatlike structures which engage the surface film and float the flower. This tiny flower, with its upraised stamens and pollen mass, is so snugly fitted to the surface film by its 3 broad areas of contact that it is kept in equilibrium under all ordinary circumstances. They are rarely overturned, even by rather vigorous agitation of the water, but maintain a strict right angle to the surface film. So slender an object as a needle if thrust into the water among these floating flowers and slowly withdrawn will be covered by the flowers that have been drawn up with the film of water about the needle and may be seen standing out radially from it on all sides. Once overthrown, however, they are not again righted, but lie partly under water.

This definite engagement with the surface film does not hinder the free movement of the staminate flowers on the water. In open areas they are caught by every passing breeze and are hurried along the surface of the water. On windy days they go scudding by the observer like tiny flecks of foam. Where the plants grow abundantly they often mass along the windward shores in broad zones of snowy white (fig. 1).

The anthers dehisce before the flowers open, and the sticky pollen from the pair of stamens of a given flower usually forms a single pollinium (pl. IX). Even if the products of the 2 anthers form

FIG. 1.—Floating staminate flowers along margin of East Okoboji Lake in northwestern Iowa; the dead fish shown near center of picture was about 8 inches long.

separate pollen masses, these lie so close together as to be practically tangential, and are never widely separated, as shown by KERNER (1). Seen under moderate magnification these masses of pollen gleam like clusters of pearls. The microspores, which are slightly oval in form, are about 65 μ in diameter and have a nearly smooth exine. Their adhesiveness is of great advantage in holding the pollen together until it is rubbed off against the stigmas, and doubtless assists after pollination in holding the spores to the stigmatic hairs. The pollen output is limited, averaging about 100 spores to the flower, but varying considerably.

The floating staminate flowers are carried along by the wind, and coming within the radius of the declined surface film about the pistillate flower slide into the little depression, where they are retained. In this manner possibly as many as 50 staminate flowers may be caught in a single depression, thus forming conspicuous white patches on the surface of the water. It is interesting to note how successfully these areas of associated flowers hold together even when the water is quite rough. COWLES (5) mentions these film pockets, but gives no details other than to compare them with those of *Elodea canadensis*. In this latter form, as previously described (2), the floating pollen grains are caught in the depressions that are formed about the tiny pistillate flowers. SVEDELIUS speaks of a similar "capturing" of the pollen-bearing flowers in *Enalus acoroides*, but does not attribute this to the influence of the surface film, although obviously the case closely parallels that of *Vallisneria*.

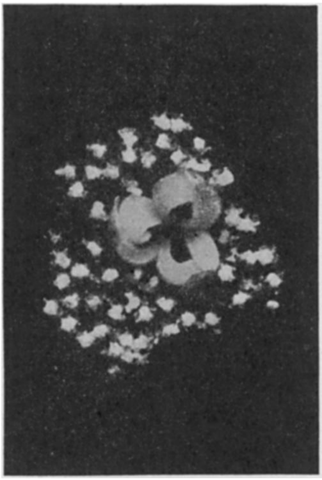


FIG. 2.*—Flowers floating on surface of water in a small aquarium surrounded by black paper; pistillate flower in center.

The sepals of the innermost of the captured staminate flowers in *Vallisneria* are of course in contact with the margins of the pistillate flower (fig. 2), but later arrivals are held back as they form only a single layer in the depression. It should be noted at this time that contact between flowers on a level water surface, such as KERNER figures, could not lead to pollen transfer, as the pollinia are upraised over the center of the flower. But with any slight declination of the film about the pistillate flower, even in quiet water, there might be contact between the innermost pollinia and the stigmas (fig. 2). Obviously, however, any movement resulting in a further depression of the pistillate flower would cause the surface film to become more abruptly declined, thus tipping the staminate flowers more sharply inward (fig. 3) and thereby

* FIGS. 2–6 constitute a series illustrating changes in relations of associated flowers floating at surface of water when subjected to submergence by pulling on scape of pistillate flower.

making conditions more favorable for pollen transfer. The upward movement of the water due to a passing wave might serve to temporarily depress the floating pistillate flower weighted by its long stalk. Should the movement be sufficient to make taut the anchoring scape, even for an instant, the depression would become cuplike, with the inner staminate flowers standing at right angles to its nearly vertical walls (fig. 4). Many of the pollen masses would thus be forced directly into the stigmas, although the outer ones would still be held back at some distance. At a certain stage of depression, however, the lateral pressure of the water breaks the surface film above the flower; the sides of the cup snap together, roofing it over; and a considerable number of staminate flowers, with the pistillate flower, are thus shut tightly together in a common bubble beneath the surface of the water (fig. 5). It should be noted that this process has completely overturned the staminate flowers, and that these are now inverted upon the pistillate flower, with their pollen masses pressed sharply into the stigmatic surfaces. The photograph for fig. 5 was taken through perhaps a centimeter of water, and shows the out-turned bases of the staminate flowers lining the bubble as seen from above. To the right may be seen a number of free floating staminate flowers that were released from the depression as the flowers disappeared beneath the surface.

FIG. 3.—Positions assumed with slight tension on scape of pistillate flower.

Release of the tension on the scape permits the flowers to come again to the surface; the bubble breaks, and most of the flowers resume their original relations at the surface of the water (fig. 6). Examination, however, shows numerous pollen grains or even entire staminate flowers scattered over the surface of the stigmas. Fig. 6 shows that the group of free floating staminate flowers, released when the group was submerged, has again entered the film pocket. This resulted from being blown into the radius of the declined surface.

Each passing wave thus brings a shift in the position of the flowers and furthers the wearing away of the pollinia upon the stigmas. During the time that the pistillate flower is at the surface the events outlined may be repeated hundreds of times with varying degrees of submergence. At all times, of course, there may be additions to the group from the free floating staminate flowers. Attention should be directed to the fact that any degree of depression is helpful, and that complete submergence, although this probably occurs frequently, is not necessary to adequate pollination.

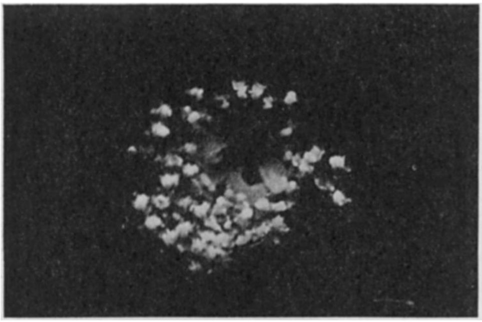


FIG. 4.—Pistillate flower has been pulled farther down in water; depression is cup-shaped, and staminate flowers stand at right angles to the verticle walls.

When the pistillate flower is finally withdrawn into the water by the coiling of the scape, numerous pollen-bearing flowers may be trapped in the bubble of air that forms about the retreating floral parts as they disappear beneath the surface. As the volume of imprisoned air is gradually dissolved by the water, the pollinia would be pressed more and more strongly into the stigmas. Observations on isolated patches of pistillate plants show that the scapes will coil somewhat without pollination, so the retreat of the seed-bearing flower is the final step in pollination if the pollen-bearing flowers are present. At the first favorable opportunity the writer plans to make a study of the flowering habits of marked plants in the field to determine the length of time the flowers remain at the surface, and the influence of pollination upon the time of their retreat.

Despite the dioecism and complete separation of the flowers in *Vallisneria*, pollination seems to take place with remarkable certainty, provided both kinds of flowers are near together in the same body of water. No doubt the pollen-bearing flowers often ride the surface of the water for considerable distances. They will float for days, and the pollen seems to withstand desiccation for a long time. In our laboratory aquaria the decline of microspores seems to be due to the attacks of fungi, and collections from the field often show hyphae among the spores.

From 200 to 450 ovules line the walls of the ovary, so that the entire pollen output of several staminate flowers would be necessary for fertilization, even if all the spores germinated. Fertilization seems to take place with certainty, for few ovules fail to develop into seeds. Scores of supernumerary pollen tubes are frequently seen lining the walls or wandering through the ovarian chamber among the ovules. Many of these meandering pollen tubes form enlargements at their distal ends similar to those previously reported for *Elodea canadensis* (2).

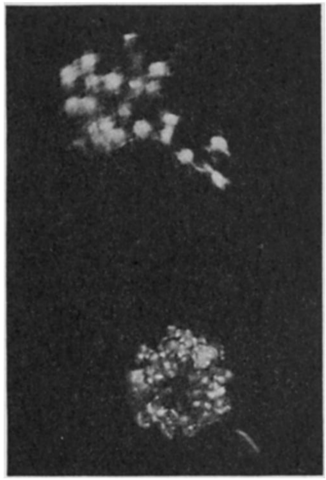


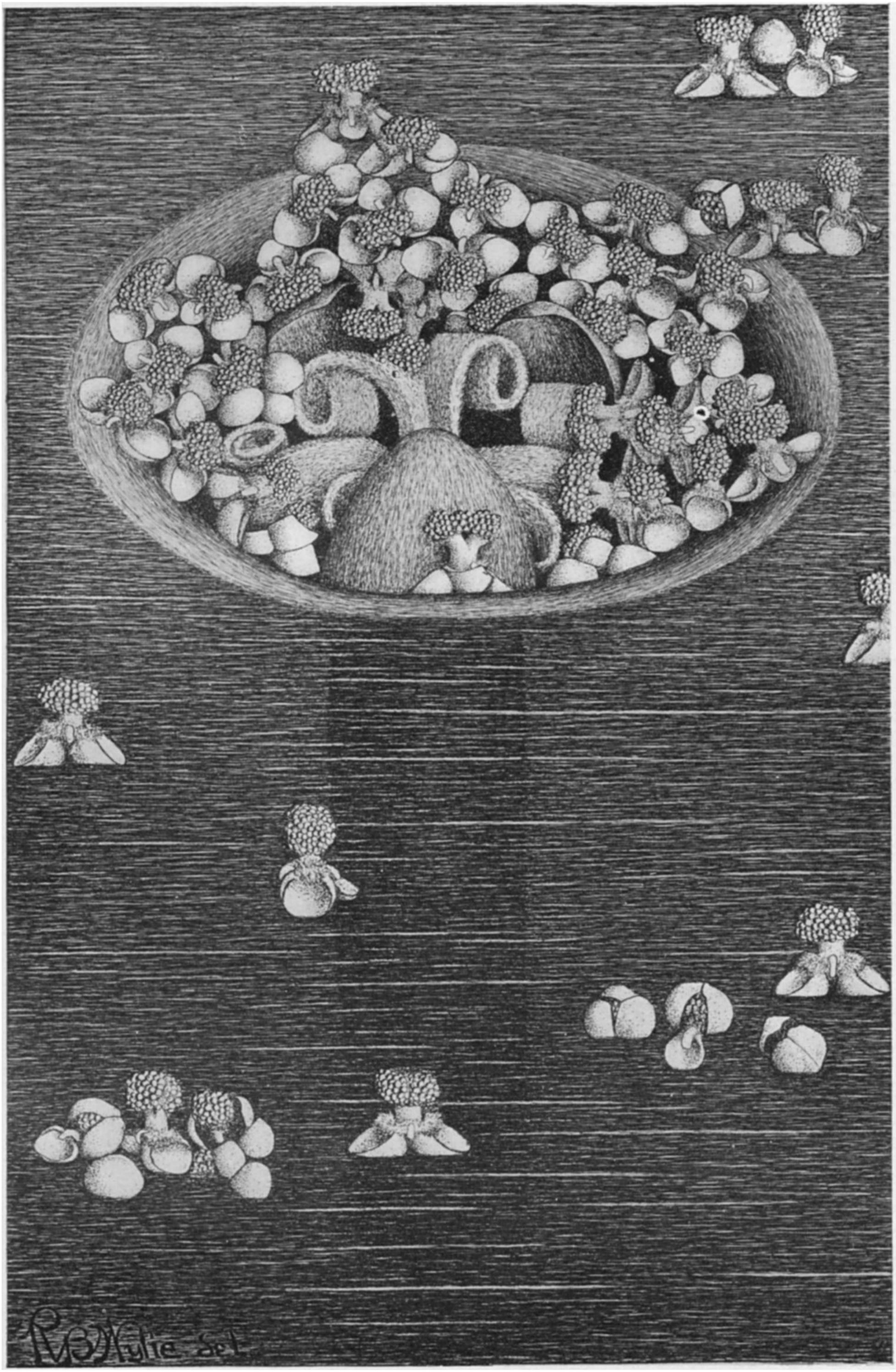
FIG. 5.—With further depression the water has closed over the flowers, now shut together in a common bubble; out-turned bases of staminate flowers may be seen on all sides, while pollen masses are being pressed directly into stigmas; near by are some pollen-bearing flowers that escaped when others were caught in the bubble (these moved during time of exposure and so are blurred in picture).

Turning now to KERNER'S widely copied figure illustrating his description of the pollination of *Vallisneria spiralis*, one is struck by the many points of contrast with the foregoing account. His illustration shows a pistillate flower with long slender ovary which, relative to the spread of the floral parts, is only about one-third of the diameter of that in our form. The spathe invests only the base of the ovary, whereas in ours it extends up almost to the sepals. The wide-spreading sepals are shown as straight, while the broad stigmas are flattened, outstanding, and raised entirely above the surface of the water. The stigmas, as shown in the figure, have margins fringed with long hairs and spread much more widely than in our plant. Finally, the whole pistillate flower in KERNER'S figure is placed in such relation to the surface of the water that it could be sustained there only on the supposition that it is supported by a stiff stem.

Similarly, KERNER has figured the staminate flower as markedly different from ours. It is represented as having 3 equal and symmetrically arranged sepals; the stamens are figured with long filaments at right angles and protruding beyond the margins of the sepals. Tiny clusters of pollen grains crown these wide-spreading filaments, carried after the fashion of the spar torpedo well over the margins of the flower. Compared with its companion blossom, the staminate flower is figured as many times larger than in our plant.

FIG. 6.—Release of tension on the scape has permitted submerged flowers to come again to surface; pollen and some entire staminate flowers may be seen on stigmas.

These and many other minor points of difference suggest that KERNER'S account is highly generalized, and perhaps intended to convey only a general account of the pollination in this plant. It may only be accidental that most of the departures from the conditions found in our plant are necessary to make possible his proposed plan of pollen transfer. On the other hand, it may be that the European plant is essentially different from ours of the same name; if so, ours should be described as another species. That there may be considerable difference between the forms on the two continents is further supported by TURPIN'S (6) figures, which show slender stamens somewhat divergent, and stigmas very different from those found in our form. In so far as one can depend upon published figures, it would seem that rather widely divergent plants are included in the species *Vallisneria spiralis*.



WYLIE on VALLISNERIA

The writer would welcome photographs, drawings, or specimens from distant regions for purposes of comparison.

In conclusion, it seems clear that *Vallisneria* offers a remarkable series of specializations mainly related to pollination at the surface of the water. A few aquatic plants have solved the problems of pollen transfer under water, and so may carry out their entire life history as submersed plants. A good example is seen in *Ceratophyllum demersum* L., which is pollinated below the surface and so may flourish at considerable depths in clear water. Neither *Vallisneria* nor *Elodea* shows any evidence of transition to subsurface modes of pollination, although this would seem to be a desirable goal for all aquatic flowering plants. On the contrary, they are perhaps carried further and further from this possible habit by their devices favoring pollination in air. Their specializations not only bespeak long association with water, but also constitute a remarkable series of adaptations to pollination at its upper limit through the agency of the surface film.

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EXPLANATION OF PLATE IX

A general drawing representing a group of associated flowers as they appear when slightly depressed; free floating staminate flowers outside the depression.