considered sufficiently distinct from the rest of the genus to be recognized as a subgeneric group designated as *Anglorota*. A specimen illustrated earlier by Reinhardt Thiessen shows sufficient agreement with *M. anglica* to be described as a variety of that species and indicates best how closely American and European forms are related.

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POLLINATION AND ITS INFLUENCES ON THE BEHAVIOR OF THE PISTILLATE FLOWER IN VALLISNERIA SPIRALIS [1]

S. B. Kausik

VALLISNERIA SPIRALIS L., a submerged aquatic belonging to the order Helobiales, has long been known as a classic example of a unique type of pollination first described by Kerner (1891). Twenty years have elapsed since Wylie (1917) studied the American form[2] of this plant and gave a vivid account of the processes involved in the transfer of pollen from the staminate flowers to the stigmatic lobes of the pistillate flowers on the surface of the water. The following account presents the same aspect in the life history based on a form of *Vallisneria* which grows in India and shows certain essential departures from the earlier accounts by Kerner and Wylie. This paper also includes a study of the behavior of the pistillate flowers both prior to and after pollination.

The writer recently noticed large patches of *Vallisneria spiralis* growing in a small lake adjoining the Government Horticultural Gardens, Lal Bagh, Bangalore, India. Many pistillate flowers had reached the surface of the water and were disposed more or less slantingly, exposing their stigmatic lobes and causing slight depressions of the surface of the water. During quieter periods the staminate flowers glided into these depressions and were grouped together in contact with the stigmatic lobes (fig. 1). But with the formation of waves, the clusters of staminate flowers generally drifted away from the pistillate flowers. This observation suggested that there might be departures from the account of pollination by Wylie (1917). Further, the flowers themselves were found to be rather different from his descriptions. Consequently, a detailed study of pollination and also of the structure of the

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The writer wishes to state that he enjoyed correspondence with Professor Robert B. Wylie, of the State University of Iowa, U. S. A., who has offered helpful suggestions; he wishes also to thank Professor M. A. Sampathkumaran, of the University of Mysore, Bangalore, India, for his kindness throughout the progress of this study and for helpful criticism at various times.

[2] In discussing the diagnostic character of the American form of *Vallisneria*, Fernald (1918) states that treated as a species it is *V. americana* Michaux, or as a variety it would be *V. spiralis*, var. *americana* (Michx.) Torr.

flowers was undertaken with plants in natural surroundings as well as in the laboratory.

The staminate flower is about 0.6 mm. across the recurved sepals, which are three in number and of which one is smaller. There are two stamens with slender filaments spreading apart at right angles. Each stamen bears distally, when the anther has dehisced, a mass of large pollen grains. The two masses of pollen grains of a given flower project beyond the margins of the sepals (fig. 2–4) so that the

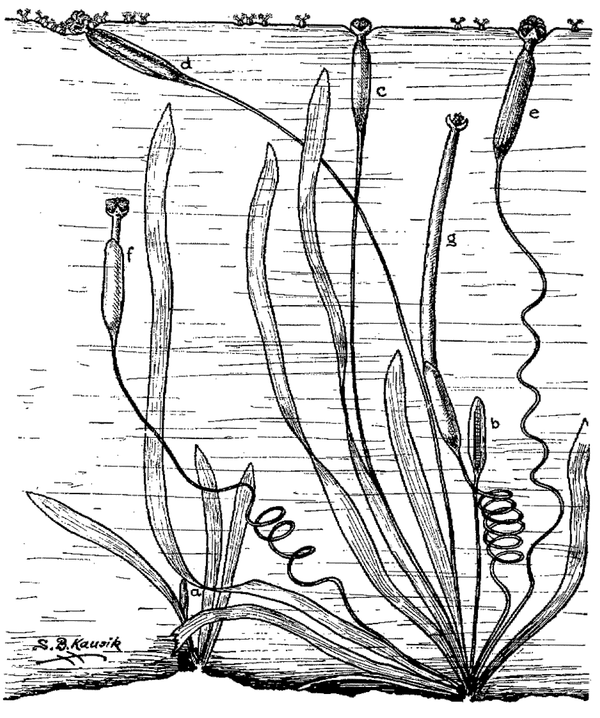

Fig. 1. General drawing of *Vallisneria spiralis* L., showing a number of freely floating staminate flowers on the surface of water and pistillate flowers in various stages of development, marked *a* to *g*.

pollen grains may immediately come in contact with the stigmas of the pistillate flower. In addition to the two stamens, the staminate flower has a rudimentary petal and a small staminodium placed on opposite sides. The staminate flower agrees in many respects with that figured by Kerner (1891), but differs in one respect—namely, that the sepals are unequal, while Kerner's figure shows them as equal and symmetrically disposed. On the other hand, a comparison with the American form studied by Wylie (1917) shows more striking differences in the floral parts. The sepals are of course similar in both, but the pointed hairs described by Wylie as occurring at the base of the stamens are absent. The most important difference, however, is that the stamens, instead of being close together and upraised in the center of the flower, forming a single mass of pollen grains, are divergent with distinct pollen masses.

There are also differences in the structure and development of the sporangia themselves. Rangasamy (1934) points out that each anther in *Vallisneria* (available locally) has usually four sporangia which are derived from independent archesporial masses, but suggests that there might be slight variations. On the other hand, Witmer (1937), in a recent study of the American form, states that each anther has normally only two sporangia and that these are formed from a common archesporium later becoming separate as growth in the stamens proceeds.

The pistillate flower also shows important differences, in size as well as in structure, when compared with that in the American plant. It has a slender inferior ovary measuring about 12 to 14 mm. in length at the time of pollination (fig. 6), while Wylie states that it is about 20 to 25 mm. in the American form. The spathe invests the ovary almost up to the base of the spreading sepals, as stated by Wylie, and later forms in the developing fruit only a partial basal investment. On the other hand, the figure by Kerner (1891) shows that the spathe leaves a considerable portion of the ovary below the sepals quite naked even at the time of pollination. Three rudimentary petals are found inside the sepals and attached at the base of the style. No staminodia are seen, but these are said to be present in the American form by both Wylie (1917) and Witmer (1937). There are three stigmas, each of which is bifid with two leaf-like fleshy expansions curling slightly outside and between the sepals to expose the inner surfaces, which are densely clothed with stigmatic hairs (fig. 7). Wylie reports that the bifid stigmas are sharply coiled in the American form when the flowers are fully open and that these coils protrude between and outside the sepals. This disposition of the stigmas in the American form favors contact between the stigmatic lobes and the pollen masses. In this connection it is of interest to note that Professor Wylie, in a recent personal communication, writes: "I am inclined to suggest that while the American *Vallisneria* does not have the stamens separated, this possible handicap is more than compensated for by the extensive stigmas which are coiled and protrude between and outside the sepals, assuming the recognition you have given to the depression of the surface film. They may possibly be as fully exposed to pollen contact as in your form in which as you say the stigmas are curled outside the sepals."

It is thus seen that the two forms are structurally very different in their flowers. While the pistillate flower in the Indian form is only half as long as that in the American form, the staminate flowers do not appreciably differ in size, being less than a millimeter across in either. The size relationship then, between the staminate and the pistillate flowers in the Indian form, is very different from that in the American form; this disparity is perhaps correlated with the difference in pollination noted for these two forms.

The plants grow along the margins of lakes in shallow water where the depth may not exceed usually about one and a half or two feet. The leaves are strap-shaped and attain a length of approximately a foot or a little more. The American plant, on the contrary, appears to be much larger, with leaves up to a meter or more in length. The pistillate flower develops under water and is brought to the surface at the time of pollination by the elongated slender scape (Fig. 1*d*). The latter forms some surplus length which places the pistillate flower in a slanting position on the surface film of water. The floral parts of the flower are exposed on the surface and on account of the weight of these, the surface film forms a slight cup-like depression about each pistillate flower. At this time staminate flowers, floating on the surface, are moved along by currents or wind and may reach these depressions, when they tumble down and perforce strike against the stigmatic lobes of the pistillate flowers (fig. 1*d*). In this act a quantity of pollen is immediately shed on the stigmatic lobes, which upon examination show loose pollen grains, as large as 50 μ, sticking to their receptive surfaces. When, however, the water is disturbed, as frequently happens by the formation of strong waves, the pistillate flowers may suffer a temporary submergence, at which time the associated staminate flowers generally lose their contact with the stigmas and drift away. But, with the passing of the wave, the pistillate flowers are again exposed in the surface depressions. The transfer of pollen to the stigmatic lobes proceeds favorably during the short intervals when the surface of water is fairly quiet between successive waves. While many staminate flowers have merely a chance of "touch and go," the majority of them perhaps never reach the pistillate flowers but are washed ashore.

While the present observations are in general agreement with the details of pollination suggested by Wylie (1917) and strongly support the emphasis laid by him on the surface film in aiding pollination, the submergence of the pistillate flowers by the formation of waves does not appear to the writer to be a prime factor in the Indian form. In describing the events in pollination, Wylie suggests that submergence is undoubtedly beneficial to pollen transfer in the American form. However he notes elsewhere in the paper: "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." The writer wishes to emphasize that pollination in the Indian form can go on uninterruptedly in the absence of submergence and in fact takes place largely during periods when the surface is not agitated by waves and strong ripples. It is, however, possible that submergence is indirectly helpful to some extent, in that it causes a dislodgement of old staminate flowers from the stigmatic lobes and thus offers chances for fresh staminate flowers to function in pollination.

The different degrees of importance attached to the submergence of the pistillate flowers in the American and the Indian forms may perhaps be properly ascribed to the relative size and structural differences in the flowers of these two forms. The divergent anthers appear to be perfectly suited to bring their pollen into immediate and direct contact with the stigmas in the surface depressions even

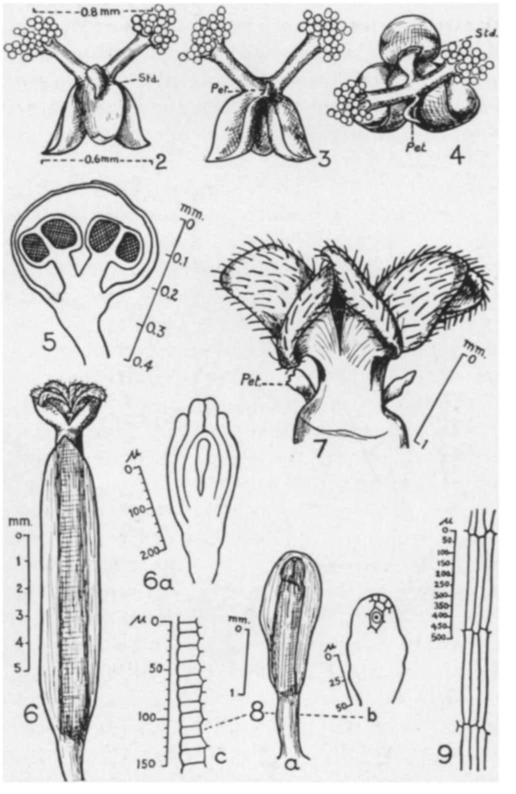

Fig. 2–9. Camera lucida tracings of the staminate and pistillate flowers at different stages of development.—Fig. 2–4. Staminate flower in different views to show details of floral parts.—Fig. 5. Outline drawing of longitudinal section of an unopened staminate flower to show divergent stamens.—Fig. 6. Pistillate flower at the time of pollination.—Fig. 6*a*. An ovule from the same, showing embryo sac in outline.—Fig. 7. Stigmatic lobes of the pistillate flowers.—Fig. 8. *a*, young pistillate flower; *b*, its ovule at the megaspore mother cell stage; *c*, the epidermal cells of the scape of same.—Fig. 9. Epidermal cells of the scape of a pistillate flower at the time of pollination to show the elongated cells. *Pet.*, Rudimentary petal; *Std.*, staminodium.

when the water is fairly still. Further, the pistillate flower is much smaller than in the American form, and it therefore presents a much smaller area at the surface of water for contact with the staminate flowers; furthermore, during submergence it is not capable of retaining the staminate flowers in such large numbers or as generally as in the American form, which has a much larger area of depression and the stigmas are sharply coiled.

The earlier work of Kerner (1891) appears to be, as already suggested by Wylie (1917), "highly generalized, and perhaps intended to convey only a general account of the pollination in this plant." Kerner has ignored the special agency of the surface film in the process of pollination and figures a level water surface with the pistillate flower held high straight above water as if by a stalk. The cup-like depression, which is so essential in capturing and retaining temporarily the staminate flowers, was entirely overlooked by him. His account of pollination appears to be based on an unsound principle, for the surface depression is a natural phenomenon formed on account of the purely physical property that the surface film of water has in relation with any floating object that is not wetted by water. Further, the arrangement of the flowers themselves on a level water surface, as depicted by him, does not seem to be conducive to adequate pollination.

Influences of pollination on the behavior of the pistillate flowers.—Turning now to the second aspect of this paper—namely, the behavior of the pistillate flowers, prior to and after pollination—the following is a description of some features noticed by the writer. The pistillate flower develops under water, and at the stage when its ovules are in the megaspore mother cell condition, it is a little over 2 mm. long, with a very short stalk measuring about a millimeter (fig. 8*a*). The stalk gradually increases in length until it brings the pistillate flower to the surface of the water. The increase in length is largely due to an elongation of the individual cells of the scape; in a number of instances it was found by measurements that the cells had increased by about 40 to 50 times their original length (fig. 8*c*, 9). It may be noted here that the pistillate flower of *Elodea* Wylie (1904) also reaches the surface of the water by cell elongation, at the time of pollination, of that part of the flower above the ovary.

When the pistillate flower has just reached the surface of the water, it is nearly vertical but later gradually assumes a more or less horizontal position by the further increase in the length of the scape. The stigmatic lobes spread out in about two to four hours, and pollination is effected in favorable circumstances in about four to six hours. After pollination the scape of the pistillate flower undergoes a spiral torsion, which is first evident at the base of the ovary. This is followed by the formation of a number of coils in the scape. These coils then draw closer and tighten, and the pistillate flower retreats under water, where the fruit is developed. Müller (1878) pointed out that the anatomical structure of the scape includes two vascular strands, of which one is smaller than the other; if the growth of these two strands, as suggested by Svedelius (1904), is different, the result would be a coiling of the scape. In a quiet aquarium where the plants were kept for observation, it was found that subsequent to pollination the pistillate flower had retreated under the surface of water by a centimeter in about three hours, and in the course of another three hours it was 7 cm. below. This rate of retreat of the pistillate flower need not, however, hold good in natural surroundings.

A change in the depth of water, as, for example, when the plants are transferred from their natural surroundings to aquaria, brings about a corresponding change in the length attained by the scapes of the developing pistillate flowers. In the case of a plant which had a number of pistillate flowers some of which had already developed into fruits in the natural surroundings, with the scapes attaining their normal length of about 46 cm., one developing young flower was marked for observations. The plant was then transferred to the aquarium where the depth of water was 16 cm.; when the marked pistillate flower finally came to the surface of the water in the aquarium, it had developed a scape only 18 cm. long. Chances for pollination were immediately offered by introducing a number of staminate flowers on the surface of the water after the stigmas had completely opened; in about three hours, during which time pollination occurred, the flower commenced to retreat under water.

If, on the other hand, pollination is prevented, as was done in other similarly marked pistillate flowers, they remain on the surface of the water for a prolonged period after which they begin to retreat, rather slowly, by the formation of only a few loose coils in the scape. Sometimes, however, the length of the scape may continue to increase afresh even after the pistillate flower is completely exposed on the surface of the water and has been lying thus for some time; in one instance it was found to have developed a scape fully 40 cm. long while the water in the aquarium was only 16 cm. deep. When chances for pollination were provided, even at this late stage, the pistillate flower behaved normally and promptly developed into a fruit. In the complete absence of pollination the flowers sank only a little under water, and the formation of the fruit was altogether suppressed. Wylie (1917) states 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." Under normal conditions following pollination the pistillate flower sooner or later retreats under water and forms the fruit.

Discussion.—In considering the importance of the surface film in pollination in *Vallisneria* it is desirable to point out the few other recorded instances of a similar nature. Cowles (1911) mentions the film pockets formed on the surface of the water but does not enter into a further discussion. Wylie (1904), in discussing the phenomenon of pollination in *Elodea canadensis*, has fully described the surface depression of the water about each flower into which slide the floating pollen grains. The case of *Elodea* is somewhat different from that of *Vallisneria*, for in the latter it is the free floating staminate flowers themselves and not pollen grains scattered loose on the surface of the water which are gathered in the surface depressions. The process of pollination, however, is essentially similar in both in that the surface depressions play an important rôle. Svedelius (1904), on the other hand, does not make any reference to the possible part played by the surface film in the pollination of *Enalus acoroides*, in which he states that the cross folds of the long and delicate petals of the pistillate flowers serve to capture and retain the staminate flowers as they arrive floating on the surface of the water. But *Enalus* presents a modified case in that the plants live in the open sea where the currents are very strong and may often reach a speed of 5 to 6 knots in an hour (Svedelius, 1904), so that a very effective device for retaining the staminate flowers for pollination would be of advantage. The most complete and also the latest treatment of the subject of surface pollination is by Wylie (1917), who has emphasized the importance of the surface film in the pollination of *Vallisneria*. Kerner (1891), as was pointed out by Wylie (1917), failed to note any surface film relations in the pollination of this plant.

The present account of pollination in *Vallisneria*, the Indian form of which differs very considerably in several essential features from the American form, is in general corroborative of the observations of Wylie (1917). It differs only in one respect which appears to the writer to be of sufficient importance to be stressed—namely, in the influence of submergence of the pistillate flowers in aiding pollination. As already noted, it seems to be the size and the structural differences in the flowers in the Indian form that are responsible for this difference. A reinvestigation of the form studied by Kerner will doubtless show it behaved very much like the Indian form, for our species seems to agree more closely with the *Vallisneria* of Europe in the plan of the staminate flowers which have the widely divergent stamens figured by Kerner and noted by Svedelius (1932). The pistillate flowers are also more like the European type and are much smaller than in the American form. The differences between the various forms are so marked as to point out the desirability of a taxonomic review of the genus. This, however, does not fall within the scope of the present study.

In concluding the present study of pollination in *Vallisneria spiralis*, the remarks of Wylie (1917) in the introduction to his paper on this interesting phase in the life history of the plant may be restated: "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."

SUMMARY

The account of pollination in *Vallisneria spiralis* presented here differs slightly from that given by Wylie (1917). While submergence of the pistillate flowers may further pollination in the American form, it is not of such significance in the smaller Indian form but may be indirectly helpful in bringing fresh staminate flowers into the depressions about the pistillate flowers. The present account, otherwise, supports the observations of Wylie with regard to the part played by the surface film forming the depressions to capture the staminate flowers. Since the Indian form is more like the European, the present findings indicate that the account of pollination by Kerner (1891) may be regarded as somewhat generalized. The differences in flower structure between the various forms from different regions call for a taxonomic review of the genus.

The second part of the paper concerns the influences of pollination on the behavior of the pistillate flowers. The period ordinarily open to pollination is several hours, and the subsequent rate of retreat of the pistillate flower under water is very slow at first, less than a centimeter per hour. Pistillate flowers in the lake had scapes 46 cm. long; when the plants were transplanted to an aquarium with water 16 cm. in depth, the scapes attained a length of only 18 cm.

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