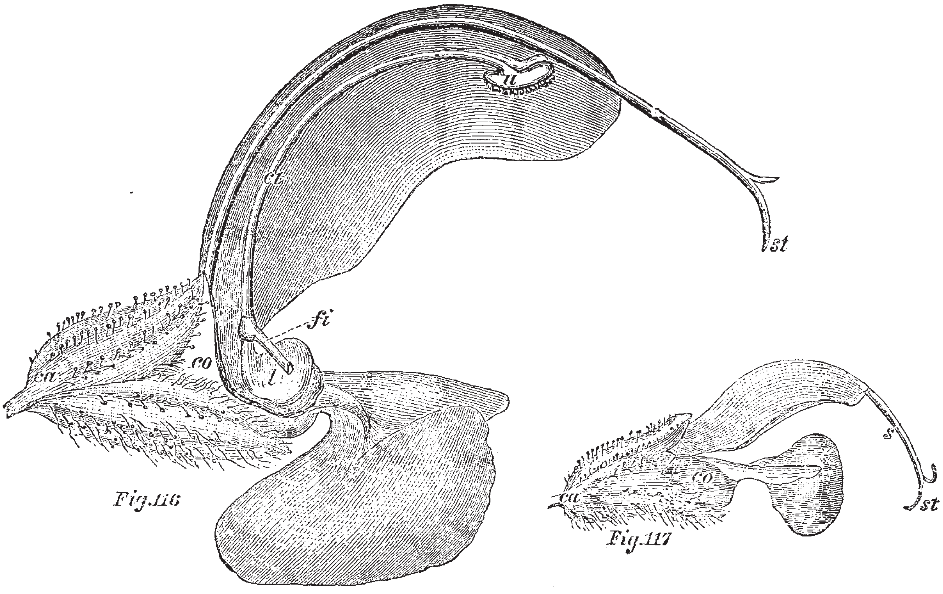
FERTILISATION OF FLOWERS BY INSECTS[1]

XVII.

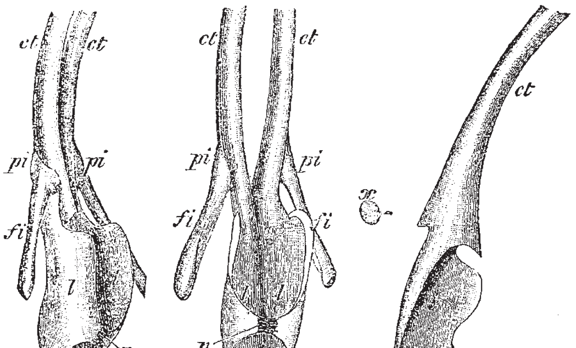
Abortion of all the Stamens in a Flower in Four Successive Periods

IN the theory of the development of the organic world useless and aborted organs are always of especial interest, as no other plausible explanation of them can be given except that they are inherited from ancestors to which, in other conditions of life, they were useful; it may therefore be worth referring to a flower in which, in four successive periods, all stamens have been aborted, and accordingly four different degrees of abortion are to be distinguished. The species in which these flowers are found, *Salvia pratensis*, is a very common one, but the flowers alluded to either do not occur at all in the usual habitats of this species, or have hitherto been overlooked by most botanists. I found them during my last excursions in the Alps in some valleys of Switzerland



FIGS. 116-129.—*Salvia pratensis.*[2] FIG. 116.—Side view of a hermaphrodite flower with the corolla partly removed ($3\frac{1}{2}$: 1). FIG. 117.—Side view of a female flower ($3\frac{1}{2}$: 1). FIG. 118.—Lower part of the two stamens of a hermaphrodite flower viewed obliquely from the front and from the right side (7 : 1). FIG. 119.—Front view of the same. FIG. 120.—Lower part of the left stamen alone seen on the inner side; the filament being hidden behind the connective. FIG. 121.—Right stamen as seen on the outside (7 : 1). FIG. 122.—Side view of a female flower, the half of the calyx and of the corolla having been removed (7 : 1). FIGS. 123-129.—Gradations of abortion of the two last stamens (7 : 1).

(Albula, Julia, Landwasser, and Landquart valley). In these, and probably many other valleys of the Alps up to 1,200–1,400 metres above the sea-level, besides the usual stems of *Salvia pratensis* with large hermaphrodite flowers, other stems with smaller purely female flowers are by no means rare. In these localities, consequently,



Salvia pratensis is in the same state as Glechoma,[3] Thymus, and some other Labiatæ in all or most of their habitats; *Salvia pratensis* is here, as Mr. Darwin calls it, in his late work,[1] a *gynodiœcious* plant. In all other gynodiœcious Labiatæ two abortions of stamens have occurred in two successive periods; in *Salvia pratensis*, as I shall show, four.

1. The Labiatæ, as well as the Scrophulariaceæ, have apparently descended from plants with five stamens. But as soon as the common ancestors of the Labiate family adapted their flowers to cross-fertilisation by bees in such a manner that their stigmas and anthers must necessarily be touched by the backs of these visitors, the uppermost of the five stamens stood in the way of the style, which for the purpose of this cross-fertilisation must stretch along the middle line of the upper side of the corolla and bend one of its two stigmatic branches downwards. Thus the uppermost stamen having become not only useless, but even directly disadvantageous, was doomed to abortion, and in the long time that has elapsed since then, has been so completely eliminated by natural selection, that not the smallest trace of it has remained, and only very exceptionally does it reappear by atavism. In those Labiatæ in which the adaptation described has been perfected, the reappearance of the fifth stamen happens, indeed, so extremely rarely that I have only once had the opportunity of seeing it, in a single flower of *Lamium album*, in which the upper lip was wanting, and, instead of it the fifth stamen was present. In the flowers of Mentha, however, in which the peculiarities of the Labiatæ just-mentioned are much less developed, the fifth stamen, as I am informed by Dr. E. Krause, of Berlin, reappears more frequently.

[1] Continued from vol. xv. p. 475.

[2] In all figures *ca* = calyx, *co* = corolla, *n* = nectary, *ov* = ovary, *s* = style, *st* = stigma, *x* = rudiments of the two aborted upper stamens, *fi* = filaments of the two lower stamens, *ct* = connective, *u* = upper anther-cell, *l* = lower anther-cell, *p* = point of union of the two metamorphosed lower anther-cells, *pi* = point of the filament on which the connective rotates.

[3] See NATURE, vol. viii., pp. 121, 143, 161.

[1] "On the Different Forms of Flowers in Plants of the Same Species."

2. Whilst the flowers of Labiatæ are generally adapted to be fertilised only by bees of a certain size, smaller ones entering the flowers without touching either the stigma or the anthers; in the genus Salvia, on the contrary, larger and smaller bees have been equally engaged in the service of intercrossing. This has been effected by the following modifications:—The stigma bends further downwards, and the connective of each of the two lower stamens has been transformed to an upright, two-armed lever, which, at its two opposite ends, bears the two anther-cells, and, by a slight pressure on either of them, turns on the filament, so that any bee entering the flower cannot but strike against the two lower anther-cells with its head, cause the connective to rotate, and thus bring the dehiscent surfaces of the upper anther-cells into close contact with its back. In direct connection with this

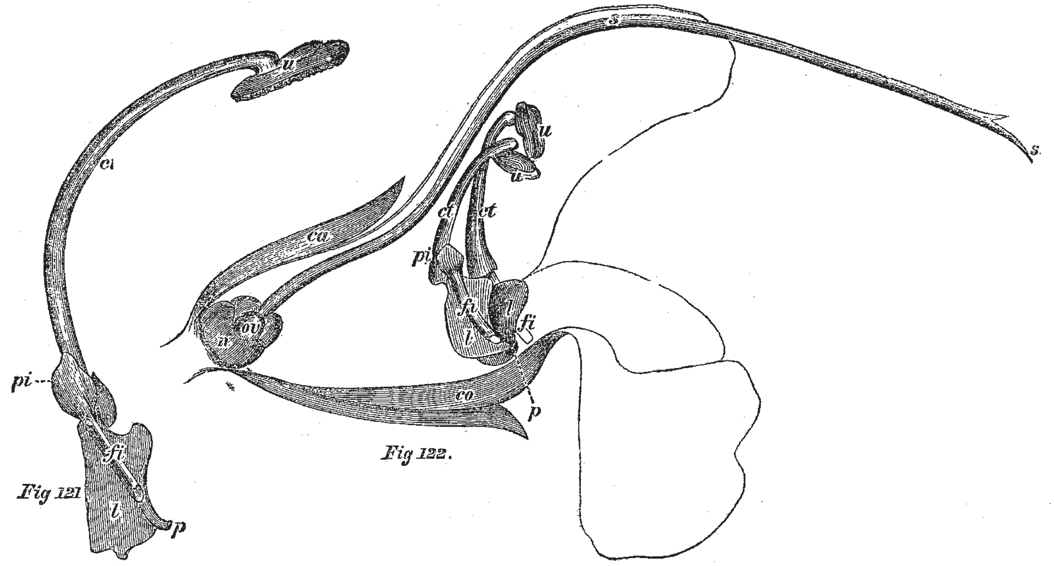


Fig 121 Fig 122.

transformation of the two lower stamens, the two upper ones, which would hinder the rotation of the levers, have aborted. But in contrast with the uppermost stamen, which has become superfluous at a much earlier period in the ancestors of the whole family Labiatæ, and has since completely disappeared, the two upper lateral stamens, which have become useless not earlier than in the ancestors of the genus Salvia, in all or most of the species of Salvia still exist in the form of two little knobs (*x*, Figs. 120-130).

3. By the transformation just-mentioned of the two lower stamens in the genus Salvia not only have the two upper stamens become a hindrance, and thus been aborted, but at the same time the lower anther-cells of the two lower stamens have been alienated from their original function

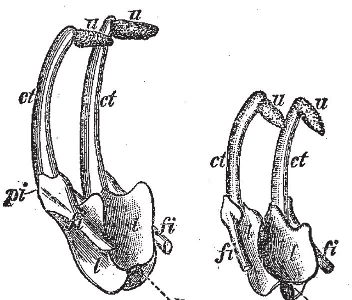


Fig 123. Fig 124.

and engaged in a new service, by which a sterilisation and metamorphosis of these has also been occasioned. *Salvia officinalis* and *pratensis* show us two steps of this further modification. In *S. officinalis*[1] the connective (*ct*, Fig. 130) is but moderately lengthened, the two lower anther-cells, although reduced in size, still commonly produce some pollen, but sometimes they are quite sterile; they are not yet grown together, but only adherent to each other so as generally to move in company. In *Salvia pratensis*, on the contrary, the two lower anther-cells are not only always completely sterile, but also metamorphosed into two concave plates (*l*, Fig. 118-120) firmly grown together in front (at the point *p*, Fig. 118-120), so that they act as a simple plate, which, when pressed by the head of a humble-bee, causes the two connectives to rotate, and brings the pollen of the two upper anther-cells into contact with the back of the visitor.

4. In the small female flowers of *Salvia pratensis*, also, whatever may have been their origin,[1] the last two

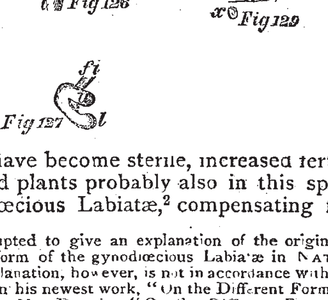


Fig 125 Fig 126 Fig 127 Fig 128 Fig 129

anther-cells have become sterile, increased fertility of the small-flowered plants probably also in this species, as in other gynodiœcious Labiatæ,[2] compensating for the de-

[1] The peculiarities of *Salvia officinalis* have been fully and excellently described and explained by Dr. William Ogle. (*Popular Science Review*, July 1869, p. 261–267.)

[1] I have attempted to give an explanation of the origin of the small-flowered female form of the gynodiœcious Labiatæ in NATURE, vol viii., p. 161. This explanation, however, is not in accordance with Mr. Darwin's views published in his newest work, "On the Different Forms of Flowers."

[2] As shown by Mr. Darwin, "On the Different Forms of Flowers," pp. 299-309.

crease in the size of the flowers and the loss of pollen. With the loss of pollen the whole machinery of the two-armed levers, which had been so gradually acquired and so exactly brought the pollen on the back of the visiting humble-bees, has become useless and begun to abort, and, according to its new origin, this last abortion, as is shown by Figs. 123-129, still offers various gradations from the perfect mechanism to an insignificant little flap. In this gradual succession of more and more reduced stamens of *Salvia pratensis*, we find some forms (Figs. 125, 126) with a striking resemblance to the stamens of *Salvia officinalis* (Fig. 130), and some of the steps which

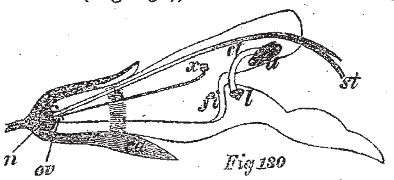


FIG. 130.—*Salvia officinalis*. Flower of *Salvia officinalis* bisected longitudinally.

are run through by this process of abortion seem to be quite analogous to those by which in former periods the stamens of *Salvia pratensis* have reached their astonishing singularity.

Briefly, the original five stamens of the flower have aborted at the following four successive periods :—

1. The uppermost stamen, in the ancestors of the family Labiatæ (complete disappearance).
2. The two upper lateral stamens, in the ancestors of the genus Salvia (reduction to little knobs).
3. The two lower anther-cells of the two lower stamens, beginning to abort in *Salvia officinalis*; abortion and metamorphosis perfected in *S. pratensis*.
4. The two upper anther-cells of the two lower stamens, in the small-flowered plants of *S. pratensis* (abortion of the pollen perfected, abortion of the anther-cells and the whole stamens beginning).

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THE RESTORATION OF THE ANCIENT SYSTEM OF TANK IRRIGATION IN CEYLON

A WORK apparently pregnant with the largest and most beneficent results to the native population of Ceylon is in process of being carried out by the Colonial Government of that island. More than a thousand years ago a system of irrigation, the most complete and remarkable that the world has ever seen was in successful operation in the Low Country, and the object which the Government has in view is to restore to something like its pristine fertility a large proportion of the immense tracts of land—many hundreds of thousands of acres in extent—that for want of water have fallen into a condition of the most utter sterility. Sir Emerson Tennant, writing twenty years ago on this subject, says, "The difficulties attendant on any attempt to bring back cultivation by the repair of the tanks are too apparent to escape notice. The system to be restored was the growth of 1,000 years of freedom, which a brief interval of anarchy sufficed to destroy, and it would require the lapse of long periods to reproduce the population and recreate the wealth in cattle and manual labour essential to realise again the agricultural prosperity which prevailed under the Singhalese dynasties. But the experiment is worthy of the beneficent rule of the British Crown under whose auspices the ancient organisation may be restored amongst the native Singhalese."

The origin of the system of irrigation spoken of dates as far back as the year 504 B.C., when, according to the Singhalese Chronicle, Mahawanso, the first tank was built in the neighbourhood of his new capital, Anuradhapoora, by Panduwasa, the second of the Hindu Kings. This was succeeded about seventy years later by two others formed in the same neighbourhood. In the year 459 A.D. the Kalawewe Tank, the largest of all, was completed. The retaining bund of this immense sheet of water is twelve miles long, and the circumference of the lake which it formed was no less than forty miles, the water being backed up for a distance of fifteen miles and conducted from the tank by means of a conduit sixty miles in length to the capital. Sir Emerson Tennant in describing these remarkable reservoirs, says, "Excepting the exaggerated dimensions of Lake Mœris in Central Egypt, which is not an artificial lake, and the mysterious basin of Al Aram in Arabia, no similar constructions formed by any race whether ancient or modern exceed in colossal magnitude the stupendous tanks of Ceylon." The same author estimates that at the time of its greatest prosperity the island contained a population of from fifteen to twenty millions, nearly all of whom must have derived their means of sustenance from irrigated lands. At the present moment, after all the care bestowed through three-quarters of a century by a paternal government, the population only amounts to 2,400,000, whilst even for this a large proportion of the food—6,000,000 bushels of rice annually among other things—has to be imported from India, and the population itself must be considered to have been somewhat unnaturally increased during the last fifty years by the stimulus of European enterprise. The mass of the people too have changed their place of residence from the interior to the neighbourhood of the sea-coast, where trading and fishing instead of rice-cultivation furnish them a livelihood. The vast areas which formerly under the magic influence of a sufficient supply of water and a hot sun, produced their two or three crops of rice in a year are now absolutely deserted, frequently not a single inhabitant surviving where once a thousand found ample means of subsistence. The city of Anaradhapoora, if its ruins afford us any means of estimating its magnitude, must have covered an immense area—no less than from thirty to forty square miles, and the population living on the spot and drawing its supplies of food from the immediate neighbourhood must have been correspondingly immense. Now it is a mere village in the midst of vast heaps of ruins.

One of the most gigantic of these early irrigation works is supposed to have been originated by Maha Sen about the year 275 A.D., and, having been enlarged by Prakrama, Bahu I., who reigned in 1153, to have received from him the name of "The Sea of Prakrama." It consisted of a series of lakes formed by an embankment twenty-four miles in length and from forty to ninety feet high, by which the water of a large river and many considerable streams was hemmed in along the base of a range of hills and so forced into the valleys that a series of lagoons or lakes was formed extending for the above-mentioned distance and frequently several miles in width. A canal five miles in length conducted the waters of "the sea" to the Minery Lake, another of the works of Maha Sen, to be mentioned presently, and a further canal from Minery led the waters to the neighbourhood of Trincomalie, in all a distance of fifty-seven miles. When it is remembered how sudden and torrential the rains are in a country like Ceylon—the writer has known 18 inches of rainfall in forty-eight hours over a very large extent of country, and at one spot as much as 18·9 inches in twenty-four hours,—we cannot too much admire the vastness of such a work and the skill which enabled the native engineers to use the natural features of the country in such a manner that for a distance of twenty-four miles a single embankment sufficed not only to hem in the water for purposes of irrigation but also to provide a water-way for the transport of produce and merchandise. Along the whole course of this embankment and canal and wherever its tributaries carried the life-giving water there would be without doubt a teeming population; for irrigable land in