

X. *On the Functions and Structure of the Rostellum of Listera ovata.*

By J. D. HOOKER, M.D., F.R.S. &c.

Received June 15,—Read June 15, 1854.

MY attention having been directed by the Rev. Professor HENSLOW, to a remarkable irritability of the rostellum in a common English orchideous plant, the *Listera ovata*, I have taken the earliest opportunity of following up his observations on the living plant, and of dissecting the organ in question; an account of the anatomy and functions of which I have now the honour of laying before the Royal Society.

The rostellum of *Listera ovata* is a broad, blunt, tongue-shaped organ, terminating the column, and projecting forwards, below the anther, and above the stigma. Soon after the flower opens, if the rostellum be touched or irritated, two white viscid masses are instantaneously protruded,—one from each side of the apex; these coalesce and form a considerable gland-like body, which attaches itself at once to the bases of the pollen-masses, and usually continues firmly to adhere to the apex of the rostellum also.

Such are the effects of artificial irritation; and a careful inspection of a great number of flowers proves, that in a state of nature this glandular secretion secures the impregnation of the plant, by freeing the pollen-masses from the anther-case, and retaining them on the rostellum, where they break up, and the granules falling over the edges of the latter become applied to the stigmatic surface.

The form and position of the labellum seems also to be of considerable importance in this operation. This organ is attached to the base of the column by a rather narrow claw, beyond which it is bent upwards, so that its anterior surface is brought immediately in front of the rostellum. Soon after the flower opens, a viscid fluid is secreted along the mesial line of the labellum, which retains the pollen-masses when these have accidentally become detached from the anther-case previous to the emission of the viscous masses from the rostellum. In some flowers I also found that the viscous masses had been projected with such force from the apex of the rostellum, that they had carried the pollen-masses with themselves beyond that organ, and had alighted on the viscid surface of the labellum, where they were retained by their bases, whilst their apices were brought into contact with the stigma.

The structure of the rostellum in *Listera ovata* is extremely curious, and, as far as I am aware, quite unique in the Order, though it is highly probable that a similar organization will be found in allied species and genera. From its earliest appearance in the young bud (as a simple transversely elongated cellular ridge) to its fully-formed condition, it undergoes no morphological change of any consequence; its development

being uniform till it acquires its broad tongue-shaped form in the mature flower, when it is about $\frac{1}{20}$ th of an inch in length and breadth. In this state it is rather concave upon the upper surface, slightly raised along the mesial line, and with somewhat upturned edges and apex. The margins are tolerably thick, and the apex presents a broad central point, with a shallow sinus on either side of it. The substance is extremely soft, white, semi-transparent and pulpy. Both upper and under surfaces are marked with 30 to 40 delicate parallel striæ, which along the mesial line are straight, while those on either side of it converge towards the apex of the rostellum, the marginal ones being conformable in direction with the outline of that organ. Towards the very apex, these parallel lines are crossed by a few transverse bars (indicating their cellular origin), and at the base they rest upon, or gradually pass into, a papillose cellular tissue, which is continuous with the surface of the column. Two darker areolæ are observable at the termination of the rostellum, occupying the shallow sinus on each side the apex; and these indicate the points from which the viscous masses are ejected through the rupture of the tissue of the cavities containing them.

After the discharge of its viscous contents, the rostellum collapses considerably, its apex and margins become deflexed, and the pollen-granules are allowed to fall over on the stigma.

A transverse section of the rostellum shows that it is wholly formed of continuous longitudinal parallel loculi, corresponding in number with the striæ on the surface; these are separated by septa of excessive tenuity and transparency, but of considerable firmness, and these, as well as the walls of the loculi, present no traces of areolation or cellular structure, except towards the apex and base of the rostellum. The loculi are many times longer than broad, and are much less in width than in depth, their diameter between the two surfaces of the rostellum being about $1\frac{1}{2}$ times greater than that between the septa, whence the appearance presented by a transverse section of the whole organ is that of a galvanic trough of 30 to 40 cells.

Owing to the exceedingly pulpy and transparent character of the rostellum, its irritability, and the viscous nature of its contents, I was wholly unable to understand its structure in the living plant, and had recourse to specimens preserved in spirits three years ago by Professor HENSLOW.

On opening the loculi, each was found to contain a very elongated club-shaped body, conformable in shape to that of the loculus (whose form might hence be deduced from that of its contents). These bodies, which are the viscous secretion of the rostellum in a hardened state, were very much flattened laterally, gradually narrowed upwards into slender points, with somewhat swollen tips, slightly curved and obliquely truncated at the base. Their bases, or rather those of the loculi which contained them, rested upon the loose cellular tissue of the column, which was distended with fluid, chlorophyll and acicular raphides.

In their youngest condition these club-shaped bodies are more opaque, and appear covered with hexagonal areolæ (an indication of their cellular origin), and are com-

posed of a grumous fluid full of minute transparent chlorophyll-globules of various dimensions. As they advance to maturity, the cell-walls disappear, and the whole tissue appears more uniformly grumous; on its first discharge from the rostellum, it presents the appearance of a glairy fluid, charged with transparent granules, acicular raphides, and traces of an hexagonal cellular tissue or rete.

The expulsion of the contents of the loculi is no doubt the natural effect of the distension of the latter, which causes the rupture of the apex of the rostellum at two points. Whether the simultaneous discharge of all the loculi is wholly a mechanical, or in part a vital action, may possibly be doubtful; if the latter, it may present some analogy to the simultaneous protrusion of the tubes from all the pollen-grains forming the pollen-mass of *Asclepias Curassavica*, first indicated by Mr. BROWN. In one instance, however, I succeeded in causing the contents of each loculus to be voided separately in vermiform masses, by compressing an immature fresh rostellum in water.

Soon after its emission the viscous mass hardens, becomes reddened, and usually adheres very firmly to the apex of the rostellum. It is not acted upon by iodine beyond being faintly browned.

The membrane of which the walls of the loculi are composed is excessively thin and transparent, and presents a beautiful appearance under the microscope; each line marking the position of the septa being bordered with a band, which is composed of excessively fine, straight, oblique or wavy striæ, which are placed at right angles to the septa.

The position and function of this glandular secretion naturally recall the theory once proposed to explain the impregnation of *Orchideæ*, which assumes that operation to take place in many species of the Order through the glands at the base of the pollen-masses; I therefore sought diligently for any facts that might countenance such a supposition in *Listera*, but in vain. I was unable to detect pollen-tubes in the glandular body at any period; and I repeatedly spread the pollen over the viscous matter when under the microscope, but without any effect; on the other hand, those pollen-grains that were placed on the stigma emitted boyaux abundantly.

In a morphological point of view, the exact nature of this complicated and highly organized rostellum is not very evident; but it may be remarked, that its position would suggest a theoretical relation with the two undeveloped stigmata of the natural order, whose position may be supposed to coincide with that of each half of the rostellum. The blending of the different suppressed organs forming the column of *Listera* is, however, so complete, that in the present state of our knowledge it is perhaps safer to regard this curious organization of the rostellum as an accessory stigmatic organ, or appendage to the stigma, such as those which occur in various natural families of plants, and more or less directly facilitate the office of impregnation.

The relation of these glands to those which congenitally connect the pollen-masses of so many genera of *Orchideæ* (either directly, or indirectly by means of the caudicula) is on the other hand very evident, and the structural passage between them may be traced through those genera in which each pollen-mass has a separate gland developed at its base, in a fovea of the rostellum. Another modification of structure in the rostellum occurs in certain genera allied to *Listera*, in which that organ is described as becoming divided into two arms, through the absorption or falling away of the intervening substance.

In all these cases the special function of the rostellum appears to be the same, and they afford beautiful instances of a great variety of modifications of structure in one organ, being all adapted to the performance of one very simple function, namely the retention of the pollen-masses. With regard to the degree of complexity presented by the several modifications alluded to, it would appear, that, taking *Listera ovata* as an extreme case, a very simple form of pollen here accompanies a very complex organization of rostellum, whereas in some *Vandeæ* which have eight pollinia attached to a strap-shaped caudicula, and that again fixed congenitally by an externally developed viscid gland to the rostellum, the latter is a mere cellular protuberance. Between these remarkably contrasted forms there are very numerous and evidently intermediate grades and modifications of structure, besides a great many which have not hitherto been reduced to any theoretical law of comparative development.

Though I have given here the results of a long and very careful examination of *Listera*, I consider the subject as far from exhausted. Professor HENSLow has had the kindness to overlook my dissections and drawings, which will I trust be found tolerably faithful, but there are many minute points in this species which yet require to be carefully investigated, whilst an examination of its allies would doubtless throw much light upon the structure and functions of the many curious forms of the column in *Ophrydeæ*.

PLATE I.

- Fig. 1. Flower of *Listera ovata* with the perianth removed, before the protrusion of the gland. *a*, termination of column; *b*, anther-case; *c*, pollen-masses; *d*, rostellum; *e*, stigma; *f*, base of the labellum.
- Figs. 2 and 3. Vertical sections of two other flowers of *Listera ovata*, fig. 2 before, and fig. 3 after, the protrusion of the gland, which is shown at *d* of fig. 3. The other letters indicate the same organs as in fig. 1.
- Fig. 4. Rostellum seen from above; (*a*) the discoloured spots where the glandular masses are protruded.
- Fig. 5. Vertical section of anterior portion of column, through the rostellum (*a*), showing one loculus and its contents (*b*), and stigma (*c*).
- Fig. 6. Transverse section of rostellum. *a*, loculi; *b*, their contents *in situ* as coagulated by alcohol.
- Fig. 7. Half the rostellum with the striated wall removed. *a*, the contents of the loculi (as coagulated by alcohol); *b*, the broken septa of the loculi.
- Fig. 8. Very highly magnified view of the loculi, showing the band of transverse striæ (*a*) bordering the lines indicating the position of the septa.
- Fig. 9. Contents of the loculi.
- Fig. 10. Upper portion of one of the same, in a very immature state, showing the areolation of its surface.
- Fig. 11. Very highly magnified view of the substance of the gland on its first expulsion.
- Fig. 12. Pollen-grains.

