J. S. HENSLOW

ON THE EXAMINATION OF A HYBRID DIGITALIS

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FACSIMILE EDITION

UNIVERSITY BOTANIC GARDEN
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WITH A PREFACE BY
S. M. WALTERS

AND INTRODUCTION BY
V. H. HEYWOOD

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PREFACE AND ACKNOWLEDGEMENTS

During the early preparation for the celebration in 1981 of the 150th Anniversary of the Botanic Garden on its present site in Cambridge, I found myself being increasingly fascinated, and indeed diverted from my more immediate tasks, by the talents and qualities of John Stevens Henslow, Professor of Botany in Cambridge from 1825 to his death in 1861. I was aware, of course, that it was Henslow, young, enthusiastic and full of plans for the future, who had persuaded the University that the old, confined Walkerian Garden, which he found in a rather run-down condition on his appointment, should be replaced by a modern scientific Garden which must be large enough to display a full range of trees and shrubs, as well as all the more traditional 'herbs' of the old 'physic garden'. This story I have told, at least in outline, in the Anniversary Book entitled *The Shaping of Cambridge Botany* (C.U.P. 1981). What I did not fully appreciate, until writing the book, was the extent to which Henslow pioneered the modern scientific outlook which we take for granted today.

If Henslow's name is remembered today by more than a small circle of botanists interested in the history of their science, it is solely because of his famous pupil, Charles Darwin. The lifelong friendship between teacher and former pupil survived even the strain of the controversy about science and religion which might have caused a serious rift between them. Reading Darwin's generous but very fair acknowledgement of his debt to Henslow, we find him stressing three qualities: his enthusiasm for all natural history, his meticulous care in observing and recording and, most important of all, personal qualities of modesty and integrity which Darwin never ceased to admire.

Stimulated by Darwin's tributes to Henslow, I turned to some of the original works to see for myself, in particular, the qualities of accurate observation and description which had so impressed his pupils, and found abundant evidence of these. Nowhere are these qualities more clearly and attractively seen than in the paper on the hybrid foxglove which is the subject of this facsimile. Moreover, by a fortunate coincidence Henslow published the paper in 1831, the same year which we now celebrate as the year in which the University purchased by special Act of Parliament the site on which the Botanic Garden stands. Since I found from discussion with my colleagues that the paper was relatively unknown, I was encouraged to consider seriously producing the present facsimile so as to bring it to a wider audience. My tentative plans were helped by the sympathetic interest shown by the officers and Council of the Cambridge Philosophical Society, and especially by the then President of the Society, the late Percy Brian, F.R.S., Professor of Botany from 1968 to 1977, an interest which has been shown practically by a generous

donation from the Society of £350 towards the printing costs of the coloured plate. The main cost of printing is being borne by the Cory Fund.

In bringing this neglected paper to a wider audience, it seemed to me that an expert assessment of the position of such scientific studies of plant hybrids before the advent of the modern science of genetics might be particularly helpful. For this, I could think of no one better equipped than my friend and colleague Vernon Heywood, Professor of Botany in the University of Reading, and formerly a research student in the Cambridge Botany School. Not only has Professor Heywood an international reputation in the fields of modern taxonomy which include the phenomena of species-hybridization, but he also happens to be an expert on the genus *Digitalis* itself. I was therefore delighted when he agreed to contribute the Introduction.

To commend this book, I feel that the last word should be with Henslow, the teacher, taken from the Preface to his *Questions on the subject-matter of Sixteen Lectures in Botany* (1851): 'Whoever may be expecting to acquire a competent knowledge of this subject by merely listening to what shall be told him at lectures, will be disappointed. "How to observe" is an art to be acquired by "observing" and not by listening, or even by reading alone. The student will find himself confused rather than enlightened if he will not take the trouble to examine plants, and to compare what he sees in them with the descriptions and definitions by which they are to be recognised. If he will consent to do this, he will soon find a growing interest in the subject.'

S. M. WALTERS

October 1980

INTRODUCTION

This detailed account of a hybrid foxglove by Professor Henslow is a fascinating historical document. Not only is it a testament to his meticulous powers of analysis and observation, but it sheds some light on the attitude of botanists to the problems posed by hybrids in the early days of genetics before the mechanism of inheritance was comprehended.

Plant hybrids had been made occasionally by horticulturalists for over a century before the time at which Henslow was writing. He remarks, however, that they mostly 'seem to have been undertaken for the sole object of increasing the forms of beautiful flowers, or of modifying the flavour of delicious fruits'. Such an aim, laudable as it may seem today, was clearly not what Henslow regarded as important. Rather, he felt that attention should be directed to the 'more curious and important physiological facts elicited by the phenomenon of hybrid production'. In other words, in the absence of the coherent discipline that we today call genetics, explanations of hybridity and its significance had to be sought in physiology.

The importance of ratios in hybrid progeny and the significance of particulate inheritance were not to be appreciated until much later, although already in 1761 Koelreuter had reported the results of several hundred hybridization experiments. Indeed, Koelreuter had described a hybrid between *Digitalis lutea* and *D. purpurea* in 1777, as Henslow remarks.

Foxgloves have been common in cultivation in Britain for centuries and *D. purpurea* is, of course, native to Britain. It belongs to section *Digitalis* while *D. lutea*, which is native to Western and Central Europe, belongs to section *Tubiflorae*. The two species are known to hybridize in nature and the hybrid is known as *D.* × *purpurascens*. It is usually more similar in appearance to *D. lutea* than to *D. purpurea*, as is the hybrid which Koelreuter described (as *D. hybrida*) in 1777, and that proposed by Lindley in his monograph of the genus (*Digitalium Monographia*, 1821) as *D. lutescens*. The hybrid with *D. purpurea* as the seed parent and closely resembling it is much less frequent.

The hybrid *D.* × *purpurascens* is sterile, as are all the other inter-specific hybrids in the genus that have been attempted. Henslow notes that he was unsuccessful in fertilizing any of the ovules in his hybrid. He was intrigued by the fact that, despite the marked difference in the habit and other characteristics of the two parent species, their pollen and ovules were identical in size and shape, a fact which led him to speculate whether such a condition might be shown to be necessary for the successful production of hybrids.

Henslow gives a detailed comparison of the external morphological features of the two species and their hybrid, and illustrates these differences in four fine plates. Particularly

fascinating is his description of the pollen and germinating grains of *D. purpurea*, showing exserted membranous tubes (the *boyaux* described by Brongniart and others), taken from a withered stigma. He also observed that 'some of the granules also were marked on the surface by three blotches' – evidently the furrows of the tricolpate grains. Like his contemporaries Henslow was handicapped by the limited capabilities of the optical aids available to him. Despite this, he continues his account with a detailed examination of the internal structure of the 'organs of fructification', although he was in fact unable to perceive any differences between the internal structure of the three plants.

Henslow concludes modestly by doubting whether his contribution had shed any further light on the question of hybridity, but hopes his work will provide a useful basis for further research. It was not until the following century that many of the problems he raised were satisfactorily solved. This reprint will allow the modern reader to appreciate some of the intellectual conflicts and confusion that faced Henslow and his contemporaries, and at the same time admire the painstaking observations that characterized so much work of that time.

V. H. HEYWOOD

September 1980

VIII. *On the Examination of a Hybrid Digitalis.*

By the Rev. J. S. HENSLOW, M. A.

PROFESSOR OF BOTANY, AND SECRETARY TO THE CAMBRIDGE PHILOSOPHICAL SOCIETY.

[Read Nov. 14, 1831.]

Although the propagation of hybrid plants has been much attended to of late years by several Horticulturists in England, their experiments, for the most part, seem to have been undertaken for the sole object of encreasing the forms of beautiful flowers, or of modifying the flavour of delicious fruits. But the more curious and important physiological facts elicited by the phenomenon of hybrid productions do not appear to have received a proportionate degree of attention from those who have been engaged in these experiments. Chance having favoured me with a hybrid Digitalis during the past summer (1831), in my own garden, I employed myself, whilst it continued to flower, which was from June 19 to July 22, in daily examining its characters and anatomizing its parts of fructification. I was careful to compare my observations, with as much patience and accuracy as I can command, with the structure of its two parents. It seemed to me not unlikely that something interesting might result from a rigorous examination of this kind, or at least that its recorded details might serve as a point of departure for future observations.

The plant in question was undoubtedly a seedling from a specimen of D. lutea. I have this species and D. purpurea alone of the genus cultivated in my garden, where several plants of each had been allowed to scatter their seed, and the seedlings to grow wherever they chanced to come up. I had already remarked a singularity in the general appearance of one of these, and was watching the expansion of its flowers, when I was agreeably surprized to find it to be a decided hybrid, obviously having most of its characters exactly intermediate between those of purpurea and lutea. I had no doubt whatever of its being a seedling of lutea, from the position which it occupied in the garden: in coming up amidst several plants of this species in a spot where an old plant had grown the year before; neither had any plant of purpurea grown in the same border. Besides which, my plant exactly agrees in most particulars with a hybrid procured by Koelreuter in 1768 from seeds of lutea fertilized by the pollen of purpurea*. His account is accompanied by a rude and inaccurate figure which by no means tallies with his own description of the plant. In general habit, this hybrid approaches much nearer lutea than purpurea, Plate xv. Fig. 1. It is however decidedly taller and more robust than any specimens of the former species which my garden ever produced. Koelreuter indeed asserts that the specimens raised by him were taller than either of their parents, but he assigns a lower limit to the height of purpurea than that to which many plants of this species have attained with me. Notwithstanding its more robust character and somewhat darker hue, the eye would scarcely have recognized, upon a mere casual observation and

* Acta Acad. Petropol. Anno 1777.

before its flowering, any peculiarity sufficiently striking to class it apart from some of the varieties of lutea, but a little closer inspection immediately detected certain decided points of difference. The whole plant is not so smooth as lutea, having a decided tendency to become downy, and being completely so on the under surface of the leaves, Plate xv. Fig. 2. The glabrous surface of lutea is one great characteristic of the species; though, if the D. rigida of Lindley* is to be considered as a variety of it, which he seems to think probable, even this character fails. A few hairs are always indeed distributed here and there in the ordinary state of this plant, and seem to indicate the possibility of a transition from the one condition to the other, dependant probably on certain circumstances of soil or situation. From the ordinary condition of the leaves of lutea, however, those of the hybrid differ in a marked manner. They are even nearly as woolly on the under surface as the leaves of purpurea.

Examination of the external characters of the Hybrid.

I shall first describe the external characters of its several organs, comparing them with those of the parent plants. In Plate xvi, the corresponding parts in the fructification of the parents and of their hybrid are arranged in three columns, those of the latter occupying the middle column. A single glance of the eye will thus be sufficient to shew how exactly intermediate most of its organs are both in size and form, and in some cases also in color, to those of the two parents. There are however some remarkable deviations from this condition, which will be presently noticed.

* Lindley Digitalium Monographia, fol. Lond. 1821.

Comparative view of the external characters of the three plants represented in PLATES XV. *and* XVI.

Purpurea.	*Hybrida* (*purpureo-lutea**).	*Lutea.*
	PLATE XV.	
Biennial.	*Root.* Perennial, according to Koelreuter, and apparently so in the present instance, the plant having thrown out several offsets.	Bi-tri-ennial.
3—5 feet.	*Stem.* About 3½ feet.	2—3 feet.
1½—3 feet.	*Raceme.* About 1½ feet.	¾—1¼ feet.
less secund, and laxer.	secund, dense, nodding above.	denser.
woolly.	*Leaves.* Nearly smooth above, quite woolly	glabrous.
very soft.	below. Somewhat soft.	firmer.
crenato-dentate.	Dentate.	dentate.
petiolate, oblong.	*radical*, sub-petiolate, broadly-lanceolate, Fig. 2.	somewhat narrower.
	caulinar, sessile, narrower.	
broader and shorter.	*Bracteas;* Lanceolate.	narrower & longer.
longer than the Calyx and frequently than the bracteas.	*Pedicels.* About the length of the Calyx, and and somewhat shorter than the bracteas.	shorter than the Calyx and much shorter than the bracteas.
large, cernuous.	*Flowers*, medium size, nearly horizontal.	small, more drooping.
	PLATE XVI.	
I.	II.	III.
more spreading.	1. *Calyx*, moderately spreading in flower, afterwards connivent.	less spreading, at length more closed.
broader.	*a. sepals*, ovato-lanceolate, the odd one much narrower.	narrower.

* If a general rule for naming Hybrids should be thought advisable, perhaps it will be found convenient always to prefix the name of the plant which supplies the pollen to that which furnishes the ovule.

Purpurea.	*Hybrida (purpureo-lutea.)*	*Lutea.*
more hairy.	*b.* hairy on the margins.	less hairy.
purple.	2. *Corolla,* Yellow ground tinted with red.	yellow.
spots more numerous, deep purple, and rings paler.	A few dark purplish-red spots surrounded by a paler ring in the throat and tube.	no spots.
less hairy.	Smooth, with hairs in the mouth.	more hairy.
obscurely 4 lobed, the upper emarginate.	Distinctly 4 lobed, the lobes blunt, the uppermost notched.	4 lobes deeper, acute, the upper deeply notched.
half the length, convergent.	3. *a. Stamens* length of the tube, nearly parallel.	somewhat more extended and divergent, according to Koelreuter; but I could see no very appreciable difference.
deeper orange-yellow, with numerous spots often confluent.	*b, c: Anthers* yellow inclining to orange, with a few small scattered purple spots.	lighter yellow, no spots.
much more oblique.	Oblique to the filament, converging above.	
	d, e: Pollen White, elliptic when dry, and sperical when moist. Some of the grains obscurely three-cornered, many are abortive, but those perfected are of exactly the same size and shape as in purpurea and lutea, being somewhat less than $\frac{1}{1150}$ of an inch in diameter.	
	4. *a. Pistil,* covered below with small glandular hairs.	
few hairs.	*style* cylindrical, with a few hairs on the lower part.	hair reaches higher up.
much more acute.	*b. stigma* cloven, very obtuse.	more acute.
more ovate and more pubescent.	*c. ovarium* oblong, pubescent.	more acute and less pubescent.
much more numerous.	*d. ovules* numerous, and exactly of the same shape and size as those of purpurea and lutea.	much less numerous.

Commentary on some parts of the preceding comparison.

Raceme. Although one of the characters of lutea lies in the very decidedly secund position of the flowers, some plants have them disposed in a squarrose manner round the axis.

1. *Calyx.* About one half the number of the flowers of the hybrid had five sepals and the other half six, (Plate XVI. II. 1. *c.*) and the sections given (from *d.* to *l.*) represent the different modes of their arrangement. Figs. *d.* and *h.* however appear to be their normal condition in æstivation, the other modifications having probably resulted from inequalities introduced during the expansion of the flower. The occasional development of a sixth sepal seems to be no uncommon occurrence in this genus, and I have met with it several times in specimens of lutea and ferruginea.

2. *Corolla.* In the colored copies of Professor Lindley's monograph, there are two varieties of lutea (see his Plates XXIV and XXV) in which the corolla is tinged with red. One of these (Plate XXIV) he considers to be a hybrid plant. In shape and size it approaches very nearly to the subject of the present paper, but the other (Plate XXV) more closely resembles lutea. In his figure of lutea also, (Plate XXIII) there is a little tinge of red in the mouth of the tube, on each side the base of the lip. I have never myself found the slightest tinge of red in any specimen of lutea, though the yellow is deeper and more inclining to orange in the parts above mentioned. If however it should be quite certain that genuine specimens of lutea do occur with a tinge of red in any part of their corolla, this circumstance must considerably modify our speculations as to how far the present hybrid may have derived this color from the male parent.

Flowers of lutea are not unfrequent with the lower lip notched (Fig. γ), which indicates the presence of a supernumerary petal blended into the tube of the corolla. In about half a dozen instances I even found this petal quite free, (Fig. β) and I believe occupying the same position as the sixth sepal in the anomalous cases just referred to. In D. ferruginea, however, I have sometimes found a sixth sepal and a notched lip in the same flower. These anomalies may therefore be considered analogous phenomena among the supernumerary developments of the two organs.

3. ***Pollen.*** In comparing the action of the three pollens when immersed in water, I observed all the phenomena usually attendant on this experiment, to take place in those of purpurea and lutea: their grains quickly swelled and their granules were exploded in the form of a dense cloud (Fig. F and ζ). Two kinds of granules were also observed, the smallest and most numerous of which were too minute for me to be able to ascertain their precise shape and dimensions by the highest powers of my instruments; the others, much fewer in number, were considerably larger, and lay dispersed among the smaller like pellucid spots on a darker ground; and these might even be distinguished through the coats of the grains before their expulsion had taken place. Some pollen of purpurea taken from a withering stigma exhibited very distinctly the presence of the exserted membranous tubes (*boyaux*) described by A. Brogniart, Amici, and others, in the Ann. des Sciences, (Fig. G). Some of the granules also were marked on the surface by three blotches (Fig. H). Grains of pollen taken from the hybrid readily swelled upon immersion in water, though most of them appeared to be void of granules. Some few however certainly contained the larger

kind of granules, and I could see their explosion accompanied by successive and sudden contractions and dilatations of the grains themselves. But I could never detect any cloud of smaller granules similar to that which was exploded from the pollen of the parents, and which always proceeds from the grain by a continuous and slow emission, whereas the larger granules in the hybrid were discharged at intervals, and by separate efforts, and lay scattered at a distance from each other over the field of view (Fig. *f*.)

Koelreuter has given it as his decided opinion, derived from his numerous experiments, that true hybrids never reproduce their kind. Later experimenters have doubted this fact, and some seem to consider the question as quite settled to the contrary, at least with respect to the possibility of fertilizing a hybrid by the pollen of one or other of the parent species. But in prosecuting this enquiry we must be very cautious to keep in view the perfect distinctness of the two questions, whether it be *probable* and whether it be *possible* that hybrids should reproduce their kind. If it be *possible* that a true hybrid may do so, it may still be very *improbable*, from some deficiency in that connection of circumstances, of whatever description it be, which is essential to secure the fertilization of the ovule. We might imagine* for instance, so great a discrepancy to exist between the respective circumstances suited to the healthy action of its vegetative and reproductive functions, that although one climate may be adopted for securing the former, another might be required for obtaining

* This hypothesis is thrown out merely in the way of illustration, and not as likely to afford any solution of the cause of infertility observable in Hybrids, at least in most of them.

the latter, and thus the plant might continue to grow and flourish in one latitude, and yet be incapacitated for ripening its pollen or perfecting its ovules unless it could also thrive upon removal to another. There are certain plants, considered to be hybrids, which undoubtedly reproduce their kind freely enough; but some of these at least, if not all of them, are mere varieties of the same species. Thus Koelreuter ascertained that all the plants raised between D. purpurea and D. thapsi, by fertilizing the ovules of either by the pollen of the other, were constantly prolific, but then he also ascertained that D. thapsi itself when cultivated by him, after five generations assumed all the characters of purpurea. He consequently rightly inferred that D. thapsi was to be considered no otherwise than as a Spanish variety of the more common form of the species. If, again, it were possible for a true hybrid to be fertilized by the pollen of either of its parents, though it could produce no fertile pollen for itself, it would then evidently be in much the same condition as the female plant of any diœcious species, and its fertility might be secured by the instrumentality of insects, &c. In the present plant I repeatedly observed that the blossom always fell before the anthers on the shorter stamens had burst; and in order that this should not operate in diminishing the chance of impregnation, I touched some of the stigmas with the pollen extracted from these anthers, but without any success. Possibly however the pollen was not sufficiently ripened. I also touched other stigmas with the pollen of purpurea, and others again with that of lutea; but all these experiments failed in fertilizing any of the ovules. Koelreuter was equally unsuccessful in his attempts to fertilize this hybrid. I must here record what has appeared to me a remarkable circumstance, brought before my notice during

the prosecution of these enquiries. There were three or four plants of lutea in my garden which were quite deficient in pollen, and which nevertheless produced perfect seeds. I was unable to detect even a single grain of pollen either healthy or abortive in their anthers, though these latter organs appeared to be well formed and perfected. The ovaria of these plants indeed contained plenty of ovules, most of which I afterwards observed had been fertilized, since their seeds ripened. These plants must therefore have been fertilized by the pollen of other specimens in their neighbourhood; at least according to all our present notions on this subject. But then the ovules of the hybrid were also similarly circumstanced, and if they had been capable of receiving the same influence from other plants, there is no apparent reason why they should not have proved fertile also.

4. *Ovules.* In the parent plants, the ovules begin to grow and develop themselves immediately after the fall of the corolla, whilst in the hybrid they soon wither away. It is remarkable however, that all symptoms of decay in the ovarium are strictly limited to the ovules themselves, for even the little protuberances upon which they are seated on the placenta remain succulent, as do the various parts of the pericarp, including also the base of the style: all which continue healthy and attain their perfect dimensions, the valves alone slightly collapsing from the deficiency of the ovules in the enlarged cells. Plate XVII. Fig. 4. But the stigmatic tissue dries up, and a cavity is thus left through the upper part of the dissepiment, forming an opening between the two cells, Fig. 5. *e.* The same effect sooner or later takes place also in the seed vessels of the parents.

Recapitulation. In reflecting upon the points of resemblance and of disagreement in the organs of fructification of these three plants,

the most striking circumstance which we have hitherto noticed in their external characters, is the perfect identity in size and shape both of their pollen and of their ovules. As the respective organs which contain these bodies, viz. the anthers and the ovaria, are each proportionate to the different sizes of the three flowers themselves, it is evident that a flower of lutea must have much less pollen and many fewer ovules than one of purpurea, which in fact the most casual observation is sufficient to shew. The ovules of the hybrid also are about intermediate in number to those produced by the parents. It will be a subject worthy of future investigation, to determine whether one condition necessary for securing the hybridity of two species, require their pollen and ovules to be of the same, or of nearly the same dimensions. Except in the above instances, and in the very peculiar shape of the stigma, all the other external characters of the hybrid appear to be precisely intermediate between those of its parents. The chief physiological difference observable in the external economy of the organs of fructification seems to reside in the fall of the corolla, which in the parents does not take place till after the anthers have discharged their pollen and become perfectly withered, whereas in the hybrid the corolla falls before the anthers on the shorter stamens have burst, and when even those on the longer pair, although opened, have hardly parted with their pollen, and have not as yet become in the least withered. The style and stigma of all three appeared to comport themselves alike, that is to say, they all began to wither soon after the fall of the corolla.

Examination of the internal structure of the Organs of Fructification.

Before I begin the detail of this examination, I may at once state, that so far as I have hitherto been enabled to pursue it, I have not perceived the slightest difference between the internal structures of the three plants; and as their organization is somewhat different from any of the cases selected by Mons. A. Brogniart to illustrate his paper on the formation and developement of the embryo, the present attempt may not be without some general interest to the physiologist, independent of the objects connected with the particular enquiry for which it has been undertaken. The method which I pursued was always to examine the various parts dissected, first, in specimens of purpurea, and then to compare them with the like parts in hybrida, and lutea. Though it is possible therefore that I may accidentally have overlooked some defect and dissimilarity in the internal structure of the hybrid during this common and simultaneous examination of all the three, and may have represented in the drawings some appearance or other strictly belonging only to the anatomy of purpurea, yet I do not think such an error could very probably have occurred. As the main object in view was the direct comparison of the three plants, any striking difference at least would have been noticed, and the subject have been submitted to a rigorous re-examination.

Vessels of the Pistil. Plate XVII. Fig. 1. represents a longitudinal section of the ovarium perpendicular to the dissepiment, and consequently passing through both the cells; and Fig. 2. is another longitudinal section, at right angles to the last, and through the plane of the dissepiment, or rather, it represents the surface

obtained by tearing the ovarium asunder down the thickness of the dissepiment, which is composed of two skins with parenchymatous matter between them. The threads of vascular tissue arranged in a circle round the axis of the pedicel (*a*), after giving off veins to the calyx and corolla (*b*), and again to the pericarp (*c*), diverge on either side into the placenta (*d*), a little above its lowest point, and then ramify or subdivide through its substance into separate fibres (*d'*) which proceed directly to the bases of the ovules. Fig. 3. represents a transverse section of the upper part of the ovarium with the lower part of the style; the valve which is nearest the spectator being removed, as also are the ovules in this cell. The smaller veins (*c'*), of which more than twenty are seen rising through the pericarp, all terminate in the base of the style; but the two larger ones (*c*), which run along the loculicidal edge of the pericarp, rise through the whole length of the style. The stigmatic tissue (*e*), (Fig. 1. 2. 3.) descends down the middle of the style till it comes into contact with the summit of the placenta. When the appearances here represented are examined with the highest magnifiers, their more intimate structure is exposed, as in Plate XVIII. where Fig. 1. and 2. are two transverse sections of the pistil, of which the former corresponds to one quarter of the circumference of the ovarium represented in the lower part of Fig. 3. Plate XVII., and the latter agrees with the section through the style in the upper part of the same figure. Plate XVIII. Fig. 3. and 4. are longitudinal sections of the same organ, the former through the stigma, the latter through the summit of the ovarium where the stigmatic tissue (*e*) descends to the placenta, as in Fig. 1. Plate XVII. In these highly magnified sections all the corresponding parts are designated by the same letters as in the former figures.

The veins (*c*), (*d*), &c. are in all cases composed of bundles of tracheæ, which in the larger veins (*c*) are very numerous. I have counted sometimes between thirty and fifty combined in the construction of a single vein (*c*), a fact which would not be suspected upon a casual observation, but which becomes evident by digesting the style in nitric acid, when these elementary parts are easily separated. Their terminations are in the form of elongated cones, and they all end together, a short distance below the stigma. (See Plate XVIII. Fig. 3.) The other elementary parts of all these veins are certain extremely delicate tubes which invest the central bundle of tracheæ, and give it the appearance of being surrounded by a mucous or glutinous substance, but which under the highest powers of the microscope may be separated into these tubular vessels, whether subdivided or not by transverse diaphragms, I was unable to satisfy myself. This very delicate tissue has the same general appearance as the stigmatic tissue, which in these plants descends down the centre of the style, to the summit of the placenta. Where this latter tissue terminates in the stigma, it is indeed evidently composed of distinct cells, easily separable from each other by nitric acid, Plate XVIII. Fig. 3. (*q*). Lower down however the cells are more elongated (*r*), and lower still, where this tissue meets the placenta, I could neither detect any transverse diaphragms in it, nor even detach its cells (if they were such) from each other at their extremities by the action of nitric acid, though they were easily separated longitudinally into long filamentous strings. In this part of its course therefore the stigmatic tissue appears rather to be tubular than cellular in its structure. After this tissue has become divided into two bands, penetrating on either side through the dissepiment into the two cells, it seemed to me, upon a most careful examination, to coat

over the whole *surface* of the placenta. It is very difficult however to be quite certain of this fact, and I may be wrong; but after numerous dissections made upon the three plants, I found I could generally raise, with the point of a very fine needle, a thin gelatinous film of a delicate fibrous structure from between the ovules Fig. 4. (*e'*), which film seemed to be similarly constituted, and also continuous with the stigmatic tissue (*e*).

Cellular tissue of the Pistil. These cells are for the most part compressed into tolerably regular rhomboidal dodecahedrons, excepting in the placenta, where, as the ovarium increases, the vesicles assume that irregular character so well described and represented by Mons. A. Brogniart in the parenchyma of the leaf, (Ann. des Sc. Vol. XXI.) and they have the same sort of interstices filled with air between them as those which occur in that organ. When the style is digested in nitric acid, the separate vesicles of its cellular tissue become cylindric-oval, Fig. 5. (*o*): and I have represented an appearance (*p*) which was noticed several times upon some of these vesicles, of a faintly marked band running down one side. — Further examination may perhaps throw some additional light upon this circumstance, but at present I know not to what cause it may be ascribed.

Epidermis of the Floral Organs. Plate XVII. Fig. 6, 7. The flattened cells are of the same size in the three plants, their diameter being somewhat more than the thousandth of an inch. They vary in shape from hexagonal to quadrangular prisms bordered by straight, or waved sides. This membrane is irregularly supplied with stomata (*f*). When digested in nitric acid, the cells assume an appearance represented in Fig. 7., as though the granular matter they contain were coagulated into a nucleus, or else were enclosed in a separate internal vesicle. Whether this

appearance originate in any optical deception, I could not sufficiently satisfy myself; but if, as I am inclined to think, it does not, the fact must have been hitherto overlooked from the difficulty of detecting the true plane of junction between the contiguous cells, owing to the very great transparency of their membrane. Thus, in Fig. 6, where this epidermis is less magnified, the cells appear to be separated from each other by anastomosing veins or canals, whilst in Fig. 7. it is shewn that their true planes of junction run directly along the middle of these canals. I am however quite positive upon another point which has been a subject of dispute among physiologists; I mean the existence of a delicate homogeneous membrane investing this epidermis. Such a membrane may be distinctly separated by the action of nitric acid, from the epidermis of the corolla, filament, and style. It is faintly marked by parallel longitudinal striæ Fig. 7, (*g*), and appears to coat over the whole surface of these organs, but whether it is perforated by a fissure opposite each stoma I did ot ascertain.

Structure of the Filament. Plate XVII. Fig. 8, 9. The cellular tissue of this organ consists of elongated rhomboidal dodecahedrons, as the elongated hexagons seen in its longitudinal section sufficiently explain (Fig. 9.). A single bundle of tracheæ runs up the middle of it, invested by the peculiarly delicate fibrous tissue already noticed.

Structure of the Anthers. Plate XVII. Fig. 10—12. The fibrous cells* composing the inner coat of the anther, appeared to me quite as distinct and perfect in the hybrid as in the parents. Nor did I observe the slightest difference in the formation and

* See Purkinje "De cellulis antherarum fibrosis, &c. 4to. Vratislaviæ 1830."

condition of any part of this organ in either of the three plants. In general, a transverse section shewed the fibrous-cells to be arranged in a triple tier (Fig. 10.). These curious vessels seemed to be set, as it were, upon the sides and edges of void dodecahedral and other polyhedral spaces, as though certain original cells of these shapes had disappeared and left this framework of their structure alone standing. The triple tier is not distinguishable upon looking directly down upon the inner surface of the anther (Fig. 11.), but some of the fibrous-cells may be seen standing upon the junction-edges of the cells of the epidermis, where this membrane has been partially cleaned of the inner coating composed of them. Fig. 12. (*h*) is the appearance which they assume when detached by digestion in nitric acid: (*k*) being the cells of the epidermis, (*l*) an accidental appearance in a grain of pollen recalling somewhat of the character of the grain figured at Plate XVI. Fig. 3. H.

Structure of the Ovules. Plate XVII. Fig. 13. When the corolla is expanded, the ovules are entirely composed of a congeries of large vesicles, and their surface has a very remarkable and granulated appearance. At this period of their existence I was unable to detect any thing very precise respecting the distinction and distribution of their several parts. The foramen (*m*) however was evidently seated near the hilum, and a darker spot indicated the chalaze (*n*) to be at the opposite extremity (see also Plate XVIII. Figs. 1. and 4.) In the ovules of purpurea and lutea, there is no difficulty in tracing the separate parts of the ordinary structure, if they be examined shortly after their impregnation; but before their fertility is secured I have not hitherto been able to detect in these plants, more than in the hybrid, any thing but a homogeneous mass of cellular tissue.

Possibly I have not given this part of the investigation sufficient attention. When the ovules are digested in nitric acid, the detached cells assume an oval shape, Fig. 15. (*o*), and are yellowish. But among them I several times observed a larger cell (*p*) which was more transparent and whiter, and which I fancied might be the origin of the embryonic sack. These component parts are best exhibited by crushing the ovule between two flat pieces of glass. Fig. 14. represents a monstrosity in which an ovule was observed to stand upon a sort of pedicel.

Recapitulation. So far then as these researches have hitherto proceeded in comparing the internal structure of the floral organs of the hybrid with those of its parents, no appreciable difference has been detected. The elementary vesicles of which their cellular tissue is constructed seem to be all of the same size, and consequently it is evident that fewer of these vesicles must be employed in the conformation of any of the parts of hybrida, and still fewer in those of lutea, than in completing the corresponding parts of purpurea. But there appears to be nothing actually defective in any part of these organs in the hybrid, nothing wanting of whatever is to be found in those of the two parents. The nutritive apparatus more especially, so far as we have examined it, seems to be quite perfect, and as the functions performed by it in all three plants are precisely the same up to the period when the flower falls, there seems to be no reason for suspecting the hybrid to differ in any particular from its parents in the perfection of its conservative organs. Since however the functions of the reproductive apparatus appear to cease in the hybrid before they do in the parents, it should seem that there must be some deficiency in this part of its organization, though it has not yet been noticed. Should the Society con-

sider the details of this examination worthy their attention, I propose to myself the further satisfaction of prosecuting it afresh next summer, if another opportunity should be permitted me. Indeed I ought to add, that in the present state of this enquiry, so little additional light has been thrown upon the great questions connected with the phenomenon of hybridity, that I should hardly have felt myself justified in presenting these remarks to their notice, were it not in the hope that they might save some time and trouble to whomsoever may be inclined to take up the subject, and possess the means of carrying on the investigation of it still further.

DESCRIPTION OF THE PLATES.

PLATE XV.

THE raceme (Fig. 1.) and radical leaf (Fig. 2.) of the Hybrid.

PLATE XVI.

The various parts of the floral organs in the three plants contrasted together. The details are at pages 4 and 5.

As the same parts in the three columns are marked by corresponding letters in three alphabets, viz. in Roman capital, small Italic, and Greek characters, it will be unnecessary to refer to more than the figures in one compartment for the purpose of explaining those in the others.

1. *Calyx.* A. sepals separated and spread open: B. their marginal hairs magnified: *c.* with supernumerary sepal: *d.* to *l.*, arrangement of the sepals during inflorescence. N. B. These sections do not refer to the arrangement of the sepals in *æstivation*, which by some neglect I omitted to notice.

2. *Corolla.*

β. with supernumerary petal: γ. ditto blended with the tube and forming a notched lower lip.

3. *Male Organs.* A. is of the natural size; the rest are more or less magnified.

A. Position of the stamens in the tube of the corolla: B. a front, and C. a back view of the anthers: D. dry, and E. moistened grains of pollen, lying on squares representing the $\frac{1}{1150}$ of an inch: F. a grain exploding upon the application of moisture: G. three grains taken from off the surface of a withering stigma, with their tubes (*boyaux*) exserted: H. a grain with three lighter blotches on the surface.

4. *Female Organs.* A. is of the natural size; the rest are more or less magnified.

A. pistil: B. stigma: C. transverse section of the ovarium: D. an ovule at the period of the flowers expansion, placed on a micrometer divided to the $\frac{1}{500}$ of an inch.

Digitalis hybrida
(purpureo-lutea)

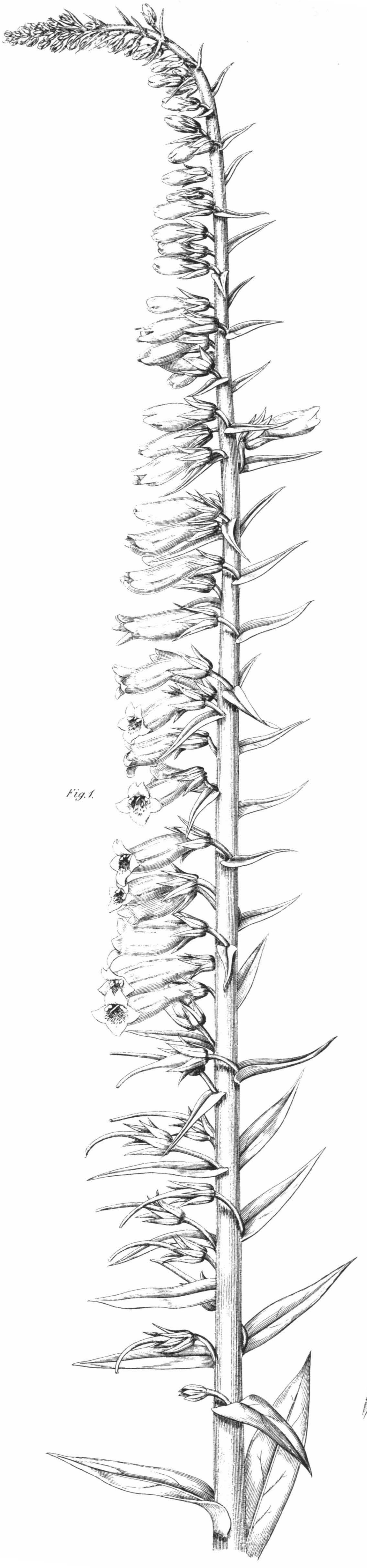


Fig. 1.

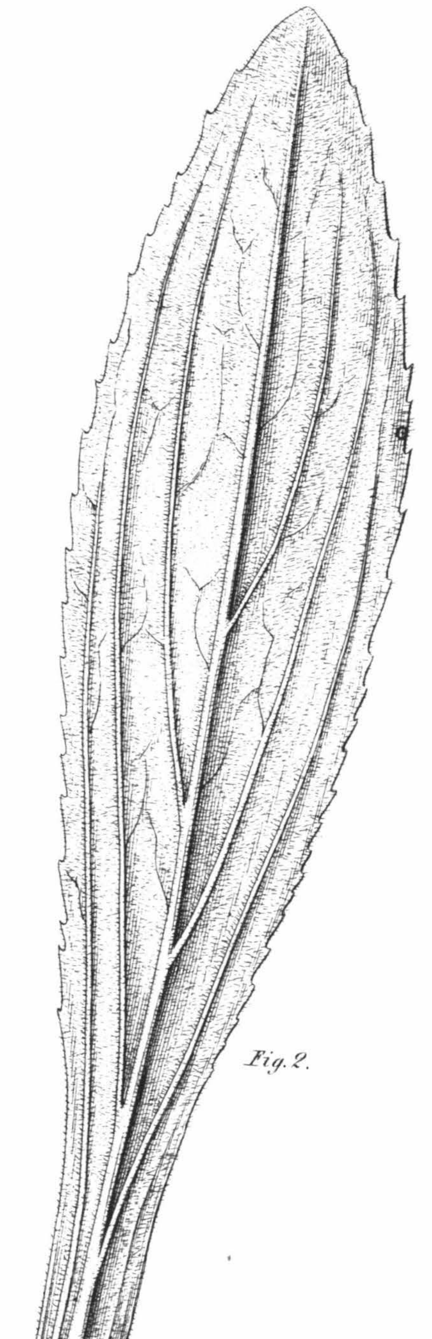
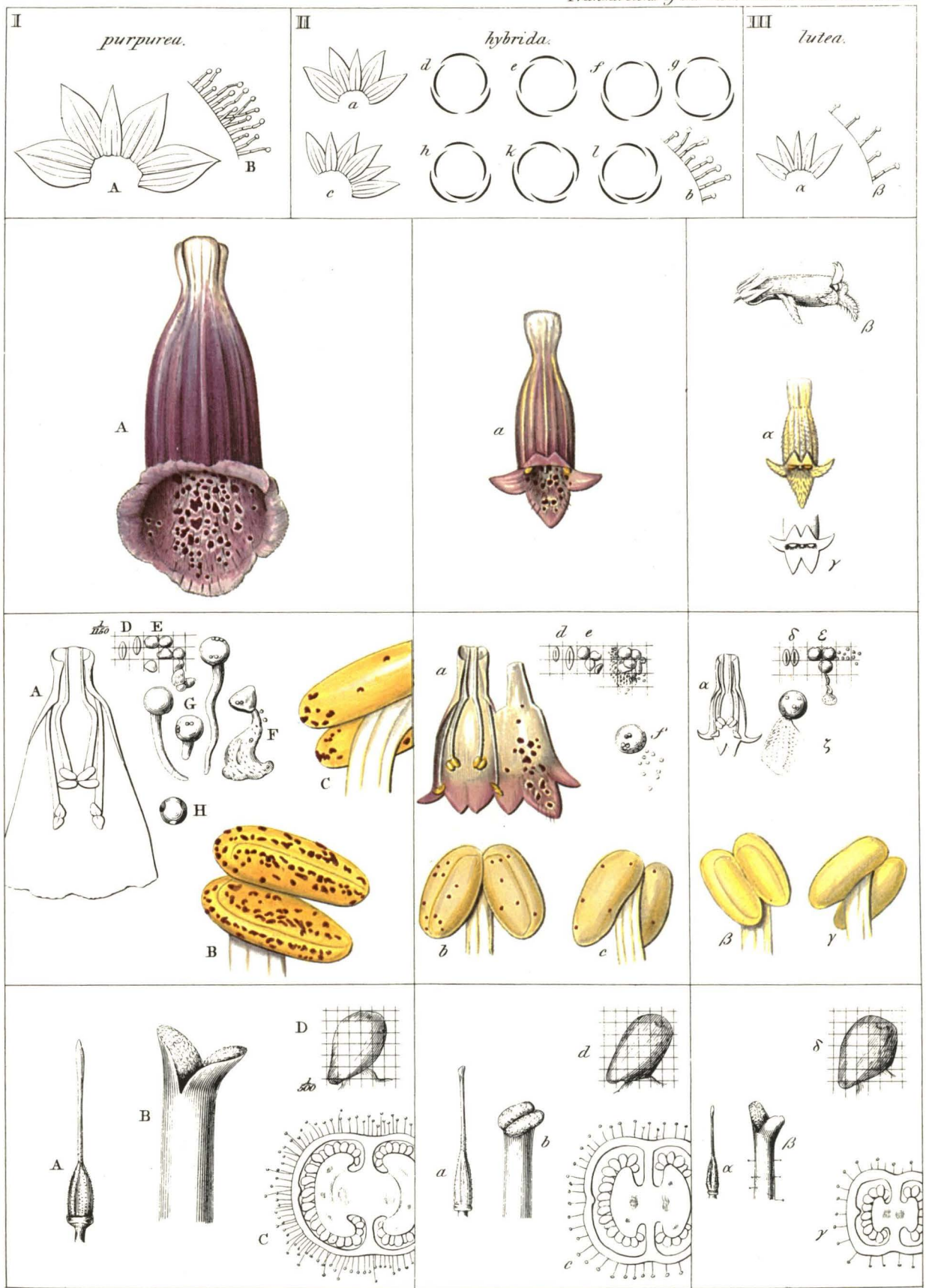


Fig. 2.

S. Henslow del.t

Ja.s De C. Sowerby sculp.t


I
purpurea.
A
B
II
hybrida.
a
b
c
d
e
f
g
h
k
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III
lutea.
α
β
1.
2.
3.
4.
A
a
α
β
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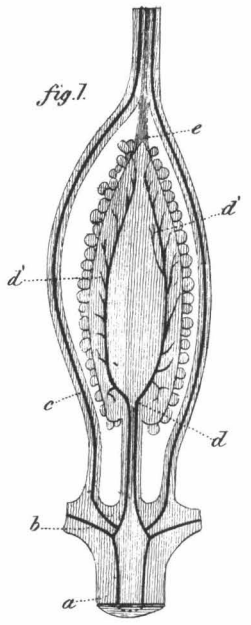
fig. 1.
e
d'
d'
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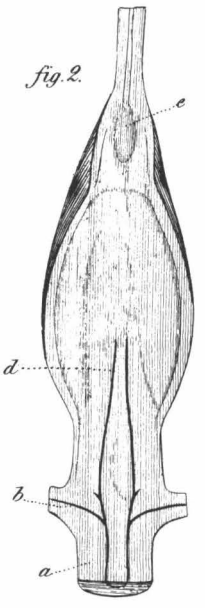
fig. 2.
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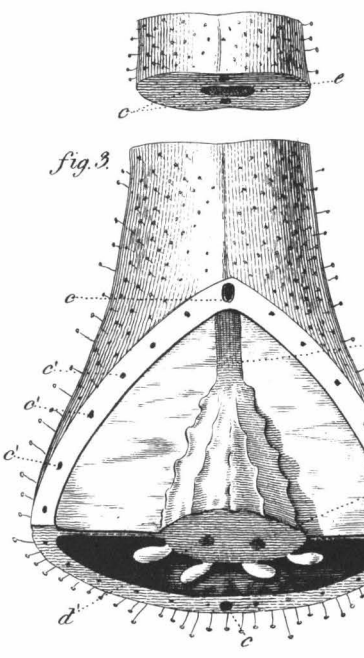
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fig. 3.
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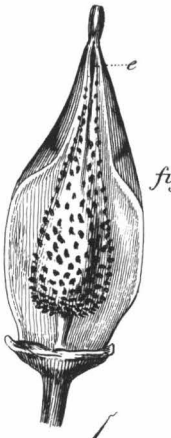
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fig. 5.


fig. 4.

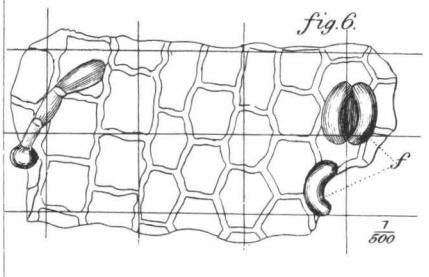
fig. 6.
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1/500

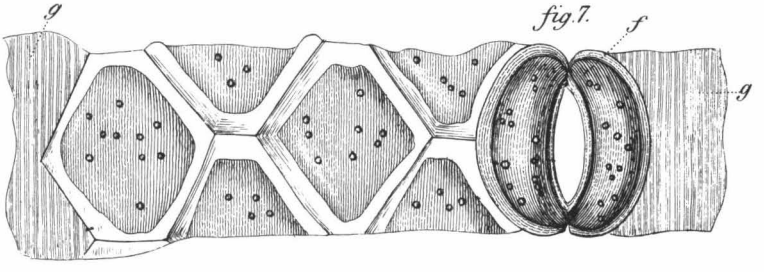
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fig. 7.
f
g

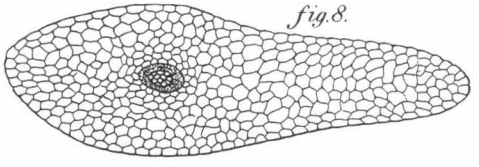
fig. 8.

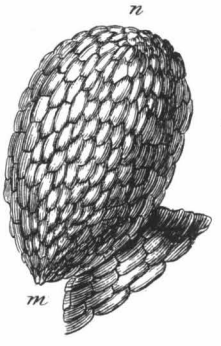
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fig. 13.
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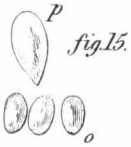
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fig. 15.
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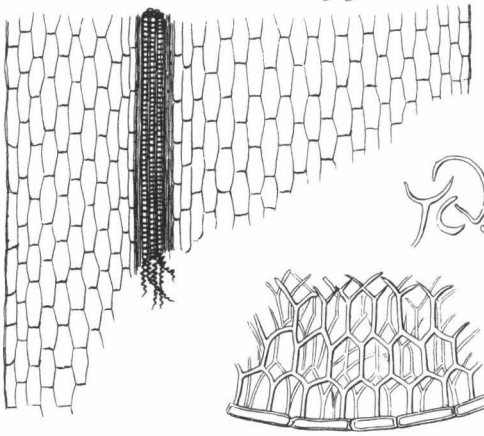
fig. 9.


fig. 12.
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k
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fig. 10.

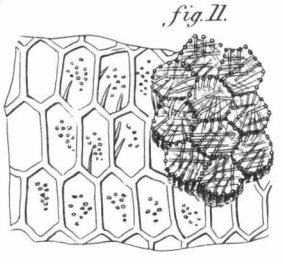


fig. 11.

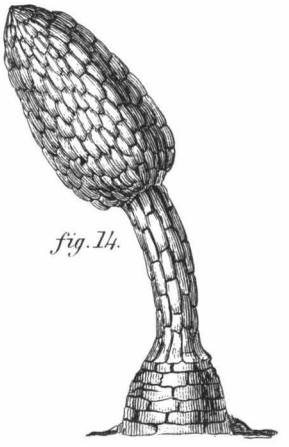
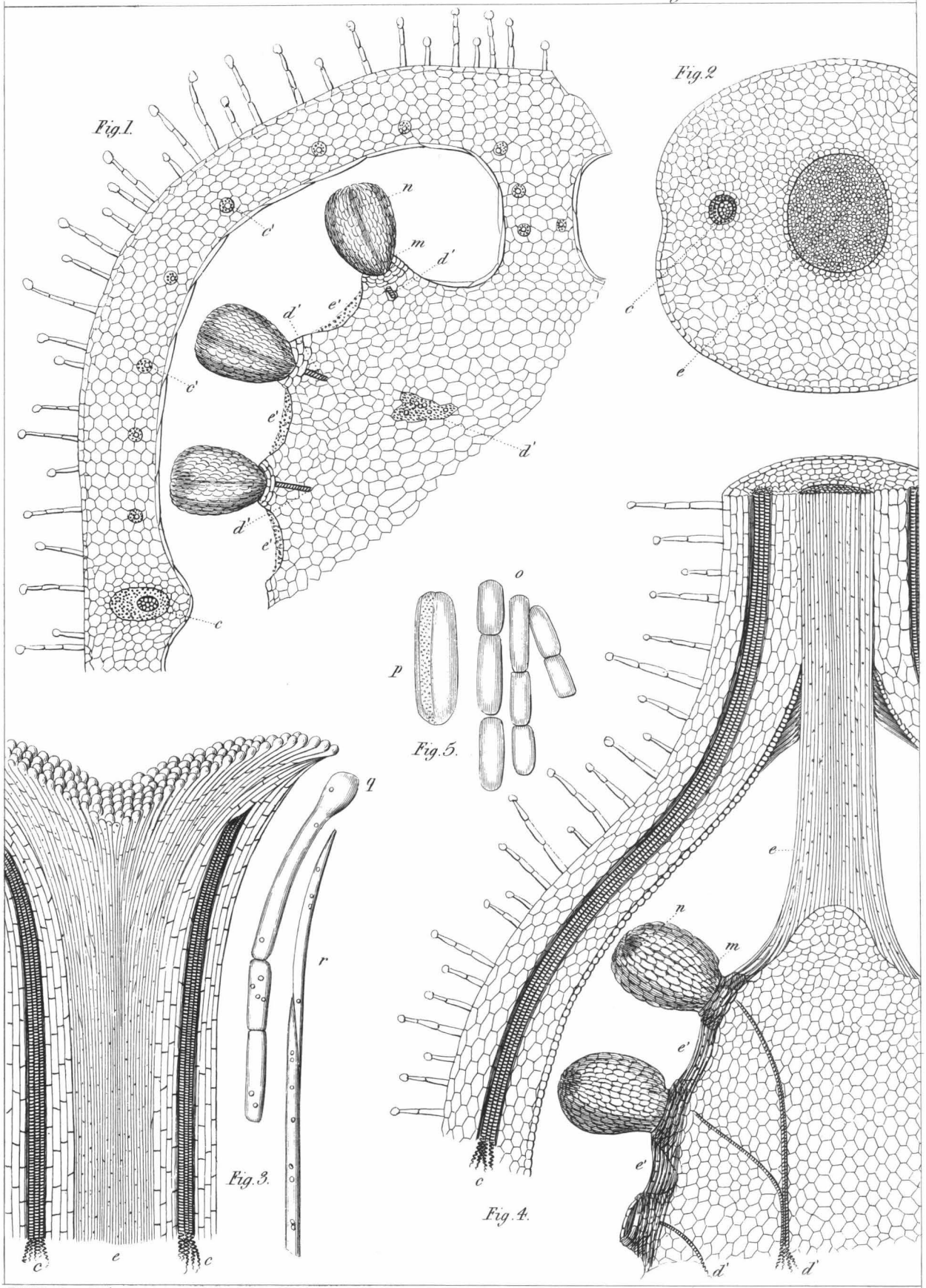


fig. 14.



L.S. Henslow del.t

Ja.s D.C. Sowerby sculp.t

PLATE XVII.

Anatomy of the parts of fructification. All the figures excepting Fig. 4, are more or less magnified. The same letter is always employed to designate the same parts in the different figures.

Fig. 1, 2. *Ovarium*, longitudinally divided; in the first case perpendicular to, and in the second down the plane of the dissepiment.

a. The pedicel with its circle of vascular bundles surrounding the axis: *b*, branches of this circle given off to the calyx and corolla: *c*, two larger bundles which run up the pericarp, along the future line of its dehiscence, and rise through the whole length of the style: *d*, separation of the vascular bundles into two bands which enter the two lobes of the placenta near their base, and rising through their substance *d'*, again separate and subdivide, giving off single vessels to the bases of the ovules: *e*, the stigmatic tissue descending through the style to the summit of the placenta.

Fig. 3. A transverse section through the summit of the ovarium, and again through the base of the style. The valve and ovules of one cell are removed. The letters designate the same parts as in the last Figure, with the additions of *c'*, small vascular bundles rising through the pericarp, all of them terminating in the base of the style.

Fig. 4. Ripened pericarp of the Hybrid, of the natural size.

Fig. 5. The same magnified, with one valve removed—exhibiting the dissepiment, and one lobe of the placenta, which is still fleshy, and covered by abortive ovules: *e* a cavity left by the drying up of the stigmatic tissue.

Fig. 6. *Epidermis* of the corolla, with a glandular hair and two stomata (*f*).

Fig. 7. The same digested in nitric acid and more highly magnified; *g*, being the investing pellicle faintly but very regularly striated.

Fig. 8, 9. *Filament*; transverse and longitudinal sections.

Fig. 10. *Anther*; a section perpendicular to its coats, exhibiting the triple tier of its fibrous cells.

Fig. 11. A fragment of the coats of the anther viewed on the inside perpendicularly to its surface, which is partly divested of the fibrous-cells.

Fig. 12. Details of the anther after it has been digested in nitric acid; *h*, fibrous-cells *k*, vesicles of the epidermis; *l*, a grain of pollen peculiarly marked.

Fig. 13. *Ovule; m*, foramen; *n*, chalaze.

Fig. 14. Monstrosity of ditto.

Fig. 15. Details of the ovule after digestion in nitric acid; *o*, the smaller vesicles composing the bulk of the ovule; *p*, a paler colored vesicle occasionally found among the former.

PLATE XVIII.

Highly magnified sections of the style and ovarium. Wherever the same letters are used in this plate as in the last they designate the same parts.

Fig. 1. Transverse section of one quarter of the upper part of the ovarium. Fig. 2. Transverse section of the style. Fig. 3. Longitudinal section of the stigma, and part of the style. Fig. 4. Longitudinal section of the base of the style and apex of the ovarium, perpendicular to the plane of the dissepiment.

c, the two large veins, or bundles of tracheæ, which rise through the whole length of the style: *c'*, the numerous smaller veins which terminate in its base: *d'*, fragments of the vascular bundles which rise into the placenta and branch off to the ovules: *e*, stigmatic tissue descending down the centre of the style to the summit of the placenta; *e'*, the same tissue coating over the *surface* of the placenta, and passing round the bases of the ovules: *m*, foramen, and *n*, chalaze, indicated by darker spots; and in Fig. 1. the position of a raphe is apparent through the ovule, by a darker band extending from the hilum to the chalaze: *q*, vesicle of the stigma: *r*, tubular vesicles of the stigmatic tissue.

Fig. 5. *o*, Vesicles of the cellular tissue of the style detached by digestion in nitric acid: *p*, one of them marked by a transverse band, when seen more highly magnified.