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On the Adaptation of *Albuca corymbosa*, Baker, and *Albuca juncifolia*, Baker, to Insect Fertilisation

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On the Adaptation of Albuca corymbosa, Baker, and Albuca juncifolia, Baker, to Insect Fertilisation. By JOHN WILSON, University of St Andrews. (Plate XII.)

(Read 8th July 1886.)

Last year Mr Alexander Wilson, the writer's brother, brought a number of bulbs of a liliaceous plant from their habitat near Port Elizabeth, Cape Colony, and during the present summer they were flowered under glass at St Andrews. One was sent to Mr Baker, Kew, who described it as a new species, under the name of *Albuca (Eualbuca) corymbosa*.*

It may be well to give here a few statistics of growth made by nine plants:—

- Average number of leaves on each bulb, 8.
- Greatest number of leaves on a single bulb, 14.
- Longest leaf, $21\frac{1}{2}$ inches.
- Breadth of leaf at base, often $\frac{1}{2}$ an inch.
- Average height of whole inflorescence, 13 inches.
- Greatest height of single inflorescence, 18 inches.
- Average number of flowers in each corymb, 9.
- Greatest number of flowers in one corymb, 12.
- Length of pedicels, $\frac{1}{2}$ –3 inches.
- Greatest number of flower-stems borne by one bulb, 3.
- Greatest number of flowers borne by one bulb, $10 + 10 + 4 = 24$.

The ground colour of the flowers is pale yellow, deepening into rich golden yellow at the apices of the perianth segments. On the outer side of each segment there is a broad central band of bright green. On the inner surface there is a similarly situated, but not so well defined band. In the fully opened flower the three outer perianth segments spread widely apart. They are then longer than the inner segments, and enclose them when the flower shuts at night and on dull days. At the apex of each of the outer segments there is a pad of tissue, thickest on the inner face (Plate XII. fig. 2, *p.*). A small area of the apex is occupied by minute papillæ. The inner segments remain erect and connivent (Plate XII. fig. 2, *is.*), forming a flask-shaped investment to the essential organs. In some cases, the space between two adjacent segments may be visible throughout their entire length (Plate XII. fig. 2), but, oftener, the margins are so close together that only a

* *Gardeners' Chronicle*, vol. xxvi. July 1886.

slit is left at the mid point. The margins bounding the slit or space are delicate and recurved. The inner segments seen from without are truncated, and have a slight terminal mesial indentation; viewed from within, each of the swollen, cucullate apices is seen to be prolonged downward into a hook-like process, along the outside of which is an area bearing golden papillæ (Plate XII. fig. 3, *is.*). The hooks fit neatly into depressions in the stigmatic surface, but do not adhere thereto. The three outer stamens (Plate XII. figs. 2, 3, *ost.*) are erect, immovable, shorter than the inner stamens. They are more or less aborted; some having pollen, others not. They stand opposite the slits existing between the inner segments, and where the slits are wide the upper portion of the stamens may protrude. The inner stamens are invariably functional. They follow, in part, the curvature of the inner segments, in the hollow of which they lie (Plate XII. figs. 3, 4, *ist.*). The upper part of the filament is broad and strap-like, widening out, and narrowing again a little distance beneath the anther. The basal portion of the filament is very broad, and immediately above this a twisting and puckering takes place, giving rise to a kind of spring (Plate XII. fig. 4, *spr.*), possessing considerable elasticity, and tending to cause the part of the filament above it to move outward. Thus, when an inner segment is pushed backward, the stamen opposite follows it until the limit of elasticity is reached, at about an angle of 45° with the axis of the flower. If not pushed too far, the inner segment reassumes its former position when the pressure is removed. The inner stamens can be pushed backwards as a whole, a hinge-like movement taking place with great readiness at their insertion. This must be done if it is desired to expose the septal glands which lie at the base of the ovary (Plate XII. fig. 5, *gl.*). These glands are hidden by the broadened basal parts of the filaments. The style is prismatic and massive. The stigma is covered with yellow papillæ, resembling those on the perianth segments, but longer. There may or may not be a tri-radiate or columnar, papillose, axial boss rising above the common stigmatic surface (Plate XII. figs. 5, 6, *pr.*), and passing outward between the deflexed portions of the inner perianth segments. At an early period of development, the inner stamens are held by the cucullate apices of the

inner segments, so that, if these be forced backwards, they carry the stamens with them. Afterwards the anthers (which dehisce introrsely) become free, owing to the more rapid growth of the inner perianth segments; but as they still lie against the inner faces of the segments, they are never in contact with the stigma. The flowers are faintly and sweetly scented.

Before the writer's experiments were commenced, he noticed a hive-bee attempt to reach the nectary of an *Albuca* flower. It first tried to penetrate to it by the openings between the inner segments, and failed. Speedily it discovered the right route. By pushing its head into the cavity formed by the apices of the inner segments, one of these yielded, and the bee entered readily, and was almost completely hidden. It is to be noted that, when a segment is pushed back, the stamen in front of it follows, and allows an insect to pass underneath the anther; the bee therefore emerged, thickly dusted with pollen about the head and back. On reaching another flower, it went at once to the right entrance. Unfortunately, the two flowers visited by the bee were not marked. The hive-bee seems to be about the size of insect fitted to fertilise this *Albuca*. The pollen carried on the insect's head will come into direct contact with the stigma of the next flower visited, especially if the latter is provided with the central prominence. The pollen on the insect's back will be deposited on the papillose area of the inner segments, which, on returning to their natural position, may convey it to the stigma. It must, however, be pointed out that, by the latter method, the carried pollen may be mixed with the pollen left by the insect in its retreat from the flower which is being visited.

With the view of demonstrating the adaptation of the flowers to cross-fertilisation, many experiments were made, the results of which are given in the table on next page.

It will be observed that the averages are unfair as regards exact comparison, inasmuch as the number of flowers used in the different series vary. The most unlooked-for case is in Series I., viz., the appearance of a fine capsule of perfect seed as the result of self-fertilisation with presumably inferior pollen. In face of the fact that the other two flowers treated in the same manner were not fertilised, and that no

corresponding success is found in Series II., III., or IV., it seems extremely probable that an accidental cross had been effected with prepotent pollen from a distinct plant. On

Results of Experiments with *Albua corymbosa*, Baker.

	No. of flowers fecundated.	No. of flowers unfertilised.	No. of flowers fertilised.	No. of seeds in the capsules.	Average No. of seeds in the capsules.	No. of seeds which germinated.	Average No. of seeds which did not germinate.
I. Pollen from semi-aborted (outer) stamens of the same flower,	3	2	1	98	98	96	2
II. Pollen from semi-aborted (outer) stamens of flower of distinct plant, . .	5	3	2	85, 87	61	32, 84	3
III. Pollen from fully developed (inner) stamens of the same flower,	9	7	2	35, 73	54	34, 58	8
IV. Pollen from fully developed (inner) stamens of different flower on the same plant,	2	2
V. Pollen from fully developed (inner) stamens of flower of distinct plant, . . .	12	2	10	{ 103, 96, 91, 84, 72, 75, —, —, 112, 110	{ 93 (nearly)	{ 99, 91, 85, 79, 70, 74, —, —, 107, 109	3.6

the other hand, it must be remembered that exceptional cases occur. In Series II. the number of unfertilised is

also larger than that of fertilised flowers. The seeds in both capsules are good, only three in each failing to germinate. In Series III. the number of unfertilised flowers, as compared with the fertilised, is very large, being 7 to 2, and from the larger capsule fifteen out of seventy-three seeds do not germinate. This series bears most significantly on the question of the cleistogamy of the flowers. Series IV. might have been expected to give other results. It is in Series V., as contrasted with Series III., that the crucial test lies. Of 12 flowers, fecundated with pollen from the functional stamens of distinct plants, only 2 are unfertilised, whereas where self-fecundation is resorted to, 7 out of 9 are unfertilised. Again, comparing the fruit in the two series, that of the former is of more uniform and greater excellence. The two capsules wanting in that series were good. One was sent to Mr Lindsay, curator of the Royal Botanic Garden, Edinburgh, and the other to Kew. Before being sent, 51 seeds were taken from the latter, and of them 49 germinated. The high vitality of the seeds in Series V. is obvious, the average number of ungerminated seeds in each of the eight pots being only 3.6.

The conclusions to be drawn from the experiments are briefly as follow:—(1) that the pollen borne by the half-aborted anthers *may* sometimes be potent, either to fertilise the same flower (?) or the flowers of a distinct plant; (2) that the pollen of the truly functional stamen of one flower may often be impotent as regards its operations on another flower of the same plant; (3) that self-impregnated flowers are almost invariably sterile; (4) that cross-fecundation almost always results in fertility.

A severe blow is dealt to the theory of the cleistogamy of this *Albuca*, by the fact that out of 97 flowers the 63 unimpregnated artificially were not fertilised. If self-fertilisation were the natural mode, surely out of this large number a few would have borne fruit.

After the completion of the experiments with *Albuca corymbosa*, a single plant of *Albuca juncifolia*, Baker,* came into flower. The latter differs conspicuously from the former in having cernuous flowers. The central (axial) projection of the stigma was invariably present. The tip of it projects so far out as to form a knob in the bottom of

* *Bot. Mag.*, t. 6395; *Gardeners' Chronicle*, 1876, p. 534.

the depression, which is bounded by the exterior faces of the deflexed apices of the inner perianth segments. As in the other species, the knob, and the portions of the segments in juxtaposition with it, are clothed with papillæ. In *A. corymbosa* the incurved apices referred to are triangular, tapering, and hook-like; in *A. juncifolia* they form a semicircular pad of relatively great thickness in the middle, and thin and flexible at the junction with the main body of the segment. The outer stamens are quite antherless. The flowers are more odorous than those of *A. corymbosa*, and the nectary occupies a much smaller area, being perhaps confined to the narrow space between the base of the filament and the ovary. The filaments are the same in both species. The structural characteristics of *A. juncifolia* indicate that it is more highly specialised than *A. corymbosa*; and the following details of the experiments tend to substantiate the belief that it is also as highly, if not more highly, adapted to cross-fertilisation. The nine flowers forming the panicle were thus dealt with:—

- 1st flower removed (eventually).
- 2nd „ impregnated with pollen from the 1st.
- 3rd „ impregnated with pollen from the 4th.
- 4th „ unimpregnated.
- 5th „ impregnated with own pollen.
- 6th „ impregnated with pollen from the 5th on the protruding tip of the stigma.
- 7th „ impregnated with own pollen after the flower had been four days open.
- 8th „ impregnated with own pollen.
- 9th „ removed.

In no instance did fertilisation take place.

EXPLANATION OF PLATE XII.

Albuca corymbosa.

- Fig. 1. *Albuca corymbosa* in flower (reduced).
- Fig. 2. A single flower, having an outer perianth segment bent downward (nat. size). *os*, outer perianth segment; *is*, inner perianth segment; *ost*, outer stamen; *p*, apical pad.
- Fig. 3. A single flower, having an inner perianth segment bent downward (nat. size). References as in fig. 2.
- Fig. 4. An inner segment, with inner stamen *in situ*. *pa*, papillose area; *spr*, spring.
- Fig. 5. Pistil. *pr*, stigmatic prominence; *gl*, septal gland.
- Fig. 6. Stigma. *pr*, stigmatic prominence.
- Fig. 7. Transverse sections of a leaf. *a*, at the base; *b* and *c*, near the apex.

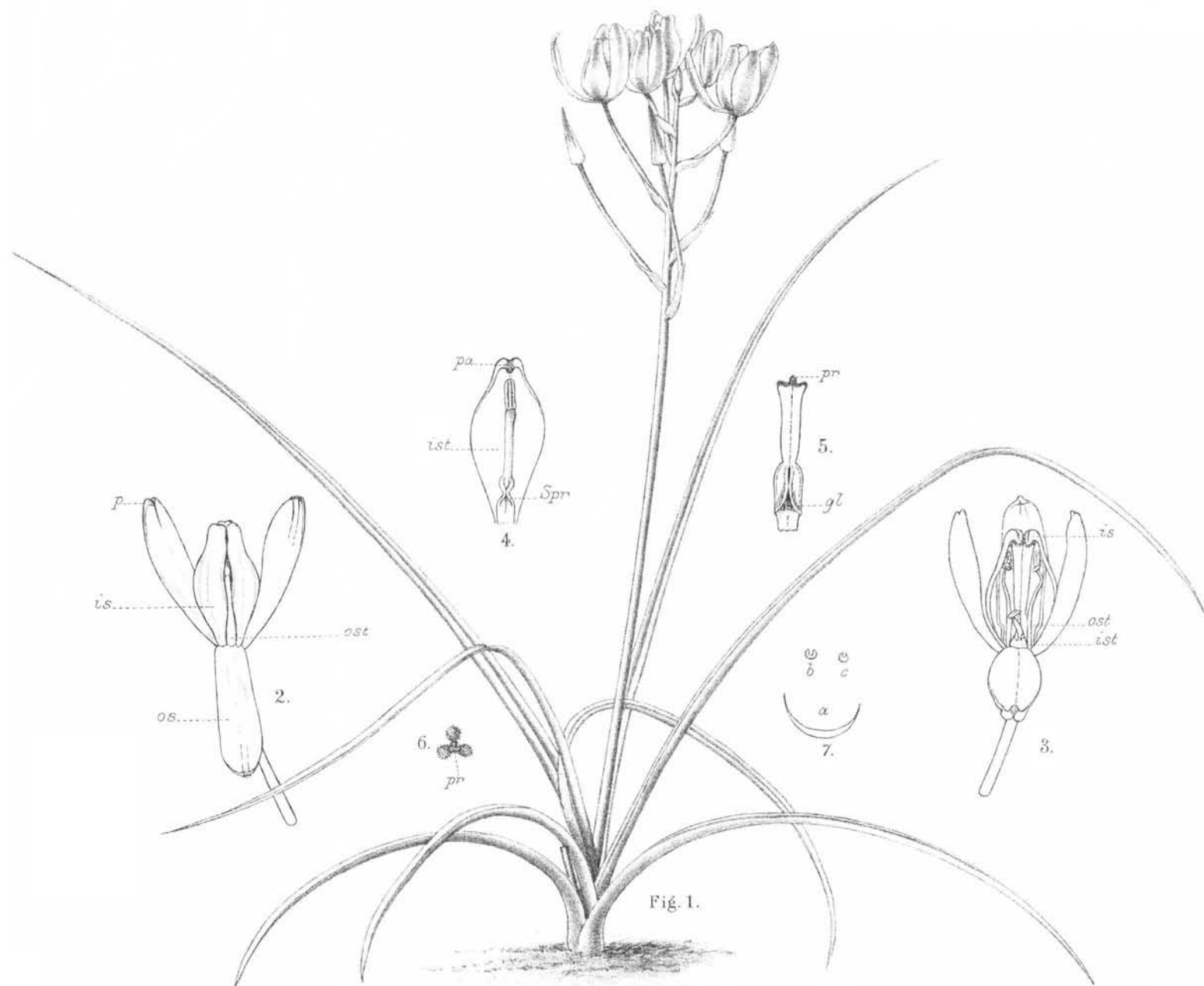


Fig. 1.

John Wilson, del.

ALBUCA CORYMBOSA.

M^r Forster & Eichen, Lith^{re} Edin^g