Notes on the Sterility and Hybridization of certain Species of *Passiflora*, *Disemma*, and *Tacsonia*. By Mr. JOHN SCOTT. Communicated by C. DARWIN, Esq., F.R.S. & L.S.

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IN the Royal Botanic Gardens of Edinburgh, plants of the *Passiflora racemosa*, *cærulea*, and *alata* have been grown for a number of years; yet Mr. M'Nab has informed me that, though annually yielding a profusion of blooms, he has never known them to produce a single seed. That this sterility originates in the impotent action of the male and female sexual elements on each other, and not merely, as might be suspected, from the pollen not reaching the stigmas, I have fully satisfied myself by continued experiments throughout the flowering seasons of 1861 and 1862. During both seasons I fertilized on each plant of the above-named species a vast number of flowers with their own pollen, but not one of them produced a single seed. I may also state, as further confirmatory of the functional impotence of at least *P. racemosa* and *P. alata*, that similar experiments have been made by one or two other young men in the Botanic Gardens with the same result. In one or two instances, indeed, in our experiments on *P. racemosa* fruits were produced; but these proved destitute of seed, the walls of the ovaries being alone developed.

A similar inveterate self-sterility in plants of the above species has been frequently noticed; and in one or two instances it has been found (but I have no books at hand for reference) that, though thus utterly impregnable to their own pollen, they are nevertheless susceptible to fertilization by that of certain allied species, while the potency of their own pollen has been proved by its effectively fertilizing other species. Accordingly, in 1863, I again instituted a series of experiments on these plants of the *Passiflora racemosa*, *cærulea*, and *alata*, in the Botanic Gardens of Edinburgh, by way of eliciting the nature of their sterility, and proving whether or not they were susceptible to reciprocal fertilization with other individuals of the same, or of allied species. The results of these experiments are so curious, that I think it will be worth while to communicate them to the Society in detail; they are as follows*.

* I am greatly indebted to Mr. J. B. Sterling for giving me pollen from a plant of the *P. alata* in the nurseries of the Messrs. Lawson and Sons, Edinburgh; and for trying experiments on this plant with its own pollen and with that of other species. I have also to express my thanks to a gentleman at

1. First for *P. racemosa* as female.—I placed pollen of the *P. alata* No. 1 upon the stigmas of ten flowers of the *P. racemosa*; seven of these set, but four of them only reached maturity, and yielded an average of 123 apparently good seeds per fruit, while the others dropped off early and contained no good seeds. Four flowers on the *P. racemosa* fertilized with pollen of the *P. alata* No. 2 resulted differently, as the ovary of not even one swelled. Again, six flowers on the *P. racemosa* fertilized with pollen of the *P. alata* No. 3 produced three fruits, two of which shanked off while the other ultimately maturing yielded 114 apparently good seeds.

By applying pollen of *P. cærulea* No. 1 to the stigmas of six flowers of the *P. racemosa*, I obtained two fruits; these contained 235 seeds, of which 197 were apparently good. Pollen of *P. cærulea* No. 2 applied to the stigmas of eight flowers of the *P. racemosa* failed to effect the swelling of even one germen. I had ultimately similar results by placing pollen of the *P. cærulea* No. 3 upon the stigmas of eight flowers of the *P. racemosa*, though I had hopes of a different result from the early swelling of three germens, but these shanked off. By applying pollen of *P. edulis* to the stigmas of six flowers of *P. racemosa*, one ovary alone swelled, but this dropped off prematurely and contained no good seeds. Again, experiments on *P. racemosa* with pollen of the *Tacsonia pinnatistipula* resulted in the abortion of all the ovaries: but I was more successful in my experiments with *P. racemosa* and *T. mollissima*, inasmuch as from six flowers of the former fertilized by pollen of the latter I got three ovaries to swell; one of these alone matured, and yielded 142 seeds, of which 22 seemed good. Lastly, I fertilized 20 flowers on the *P. racemosa* with own pollen: though, as we have above shown, it

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Keith Hall, Perthshire, for sending me pollen from plants of the *P. alata* and *P. cærulea*, and likewise for trying experiments on the former species with pollen from another individual which I sent him. The results of these experiments will be given in the sequel. For the sake of brevity, however, I will here affix numbers to each of the plants of the *P. alata* and *cærulea* experimented upon, so that I may not have further occasion for noticing the particular plant of which I may be treating; thus, *P. cærulea*, Nos. 1 & 2, refer to plants growing in the Botanic Gardens of Edinburgh; *P. cærulea*, No. 3, to a plant growing in the gardens, Keith Hall; *P. alata*, No. 1, plant growing in the Botanic Gardens, Edinburgh; *P. alata*, No. 2, plant growing in the gardens, Keith Hall; *P. alata*, No. 3, plant growing in the nurseries of the Messrs. Lawson and Sons, Edinburgh.

is perfectly susceptible of fertilization with the pollen of other species, one of these ovaries alone set, and this proved utterly void of seeds.

2. *P. cærulea* No. 1 as female.—I placed pollen of *P. cærulea* No. 2 upon the stigmas of four flowers of *P. cærulea* No. 1, and the ovaries of two of these swelled slightly, but they ultimately shanked without yielding any seed. I had more successful results with pollen of *P. cærulea* No. 3 upon the stigmas of *P. cærulea* No. 1, as, from four flowers thus treated, three ovaries set, of which only one shanked off, while the others, fully maturing, yielded conjointly 237 apparently good seeds. I also succeeded in fertilizing *P. cærulea* No. 1 with pollen of *P. racemosa*, as six flowers thus treated produced three ovaries; of these two shanked off, only one maturing; this yielded 115 seeds, of which 87 were to all appearance good. Again, by applying pollen of *P. alata* No. 1 to the stigmas of *P. cærulea* No. 1, the fruits in every case aborted; and so in experiments on *P. cærulea* No. 1 with pollen of *P. edulis*, the ovaries of not even one swelled. Lastly, I fertilized twelve flowers of the *P. cærulea* No. 1 with own pollen, but all of them dropped off without effecting the slightest development of a single ovary.

3. *P. cærulea* No. 2 as female.—I placed pollen of *P. cærulea* No. 1 upon the stigmas of four flowers of the *P. cærulea* No. 2, and thus got three ovaries to set; of these two shanked off; the other, maturing, contained 154 seeds, of which 143 seemed to be good. Again, from four flowers of the *P. cærulea* No. 2 fertilized with pollen of the *P. cærulea* No. 3, I obtained three fruits, and these yielded in all 293 seeds, of which 262 were good. I also succeeded in fertilizing *P. cærulea* No. 2 with pollen of the *P. racemosa*, as, from three flowers thus treated, I obtained one fine plump fruit; this contained 105 seeds, of which 68 were apparently good. Again, by placing pollen of *P. alata* No. 1 upon the stigmas of four flowers of the *P. cærulea* No. 2, I got one ovary to set; this, however, dropped off prematurely and contained no good seed. Lastly, on *P. cærulea* No. 2 I impregnated eight flowers with own pollen; the results, however, in accordance with my previous experiments, showed that this plant, though susceptible to fertilization by pollen of other individuals of the same species, and also by that of other species, was nevertheless utterly impregnable to its own pollen, as all the flowers thus treated dropped off without effecting the setting even of a single ovary.

4. I placed pollen of the *P. alata* No. 2 upon the stigmas of

eight flowers of the *P. alata* No. 1. The ovaries of four of these swelled for some time, but ultimately one of them shanked off, while the other three reached perfection and yielded in all 674 seeds, of which 560 appeared to be good. By the converse experiment the results were very different; thus, four flowers of the *P. alata* No. 2 were impregnated with pollen of the *P. alata* No. 1, but each of these dropped off, without affording the slightest symptoms of fertilization. Again, on the *P. alata* No. 1 I fertilized six flowers with pollen of *P. alata* No. 3; but though the ovaries of two of these set, and continued swelling for some time, they ultimately dropped prematurely and did not yield any good seed. I also had in this case the converse experiment tried for me, and from four flowers on the *P. alata* No. 3 fertilized with pollen of the *P. alata* No. 1, one ovary was induced to set; but, as in the converse case, this did not continue to swell. Seeing, however, that in either of these cases so few flowers were experimented upon, we may, I think, with justice be permitted to infer from the results that more extended experiments would show them capable of reciprocally fertilizing each other. I dissected some flowers of these three plants of *P. alata* which had been treated with each other's pollen, and found the stigmas abundantly penetrated by pollen-tubes. This fact, together with the swelling of the ovaries, shows a much higher degree of reciprocal susceptibility to each other's pollen than exists (as we shall presently see) in any one of these plants when fertilized with pollen from the same individual plant.

The following results of experiments on the *P. alata* No. 1 as female with pollen of other species may also be worthy of notice in this place, from the fact that similar or reciprocal unions have been effected by different experimenters; and, further, that in at least one of the cases to be mentioned—that of *P. alata* No. 1 by pollen of *P. racemosa*—I have found, as above shown, that fertile unions may be readily effected, while the others, either directly or indirectly, dovetail themselves into each other by curious and complex fertile conjunctions, as will be found by a careful study of my experiments as detailed. First, I placed pollen of *P. racemosa* on the stigmas of ten flowers of the *P. alata* No. 1, but these all dropped off, without so much as the ovary of one swelling. Secondly, sixteen flowers on the *P. alata* No. 1 were impregnated with pollen from the plants Nos. 1 & 2 of *P. cærulea*, but in these cases also every ovary aborted. Thirdly, in the case of *P. alata* No. 1 by pollen of *P. edulis* the results

were not materially different, as from six flowers thus treated one ovary alone set, but this did not continue swelling. Fourthly, six flowers of *P. alata* No. 1 proved impregnable to pollen of *Tacsonia mollissima*, while a similar number of flowers on the former fertilized with pollen of the *Tacsonia pinnatistipula* differed simply in the early setting of two of their ovaries, as neither continued swelling. Lastly, I applied pollen of the *Disemma Adiantoides* to the stigmas of six flowers of the *P. alata* No. 1, but this also proved ineffective, as the ovaries of not even one set.

With respect to the power of self-fertilization in the above three plants of *P. alata*, I may state that there is absolute impotence. I have already adduced evidence of this in *P. alata* No. 1 from experiments in the flowering seasons of 1861 and 1862. I repeated these in 1863 with similar results, as, from 20 flowers fertilized with own pollen, not one ovary exhibited the slightest symptoms of pollinic influence. On the plant of *P. alata* No. 2 a vast number of flowers have been from time to time fertilized, but the results showed a most inveterate self-sterility in the invariable abortion of every ovary. Again, experiments on the susceptibility of *P. alata* No. 3 to fertilization by its own pollen resulted also, according to Mr. Sterling, in the continued abortion of the ovaries. I have already stated, in previously giving the experiments on the reciprocal fertilization of *P. alata* Nos. 1 & 2, that the pollen of either, on being applied to the other's stigmas, produces pollen-tubes which freely penetrate their stigmatic tissues. In the action, however, of either stigma on its own pollen there is this material difference, that though it occasionally excites the development of the pollen-tubes, it is rarely penetrated by them.

Though the pollen of each of these plants of *P. alata* is thus utterly impotent on its own stigma, we have nevertheless shown it to be perfectly good in its relations with other individuals of the same species or with distinct species. As further illustrative, however, of the potency of the pollen of one of the above plants, I will here give the results of experiments with it on the stigmas of the *Disemma Adiantoides* and *coccinea*, both of which are also easily fertilized with their own pollen. Thus, on *D. Adiantoides* I fertilized three flowers by own pollen; each of these set, and produced fine plump ovaries, which yielded conjointly 720 good seeds. By applying pollen of *P. alata* No. 1 to six flowers of *D. Adiantoides*, I got four ovaries to set; two of these came to perfection and conjointly yielded 258 seeds, of which 46, judging

from external appearance, were good. Again, three flowers on the *D. coccinea* fertilized by own pollen produced three fine fruits and 586 good seeds. On the stigmas of six other flowers of *D. coccinea* I placed pollen of the *P. alata* No. 1, and got two ovaries to set, but only one continued swelling, and yielded in all 74 seeds, of which only 12 were plump and apparently good.

5. In the Royal Botanic Gardens of Edinburgh there are, besides these perfectly self-sterile individuals already noticed, plants of two other species of *Passiflora* worthy of a passing notice from a similar inveterate self-sterility. These are the *P. holosericea* and *P. manora*. First, for their reciprocal fertilization, I placed pollen of *P. manora* upon the stigmas of ten flowers of the *P. holosericea*; the ovaries of seven of these set, and ultimately produced, in so far as could be judged from the plump, round, palish-yellow ovaries, perfect fruits. On dissecting these, however, I was disappointed to find that the walls of the ovary had alone been developed, and that they were all destitute of aught but the veriest rudiments of seeds. I have frequently repeated this experiment, and in every instance I found that the development of the ovaria of the *P. holosericea* may thus be readily effected by the pollen of the *P. manora*, whereas it is utterly impotent in exciting the slightest development of the seeds. I likewise tried the converse experiment, and applied pollen of *P. holosericea* to the stigmas of ten flowers of the *P. manora*; of these only one ovary set, but this soon shanked off. Though I have frequently repeated this experiment, I have not again got a single ovary to set. Again, with respect to the fertilization of these species with own pollen, I may state generally that though I have thus fertilized a vast number of flowers on both plants in the successive flowering seasons of 1862 and 1863, yet in no instance did a single fruit set. I also examined the stigmas of several flowers on both plants after the application of own pollen, and invariably found that the stigmas had failed to excite the development of a single pollen-tube. On the other hand, pollen of the *P. manora* readily protrudes its tubes when placed on the stigmas of *P. holosericea*, though, as we have shown, it utterly fails in effecting the vitalization or even development of the seeds. In the converse experiments I also examined the stigmas of *P. manora* after being covered with the pollen of *P. holosericea*, and in several instances found the pollen-tubes protruding and penetrating the stigmas, though, as we have seen, they fail to effect a fertilizing influence.

6. Lastly, I have to notice the results of experiments on plants of the *Tacsonia pinnatistipula* and *mollissima* growing in the Royal Botanic Gardens of Edinburgh. It had been observed that the plant of the *T. pinnatistipula*, though annually producing a profusion of blooms, rarely produced a single fruit; and, further, that when the latter were produced the seeds were always imperfect. It thus became the subject of the following experiments. In 1862 between 100 and 200 flowers were fertilized with own pollen, yet from these only three ovaries swelled; one dropped off prematurely; the two others came to perfection, forming large, plump, orange-like fruits. On cutting these open, I found in them an abundance of seeds; but these proved all imperfect, as on examination they were found destitute alike of embryo and surrounding albuminous matter, the hard sculptured spermoderms having alone been developed. From this sterility to own pollinic influence, I determined to try these flowers with pollen of other species. Accordingly, in 1863, I placed pollen of *T. mollissima* on the stigmas of six flowers of the *T. pinnatistipula*; of these three set fruits, but two of them shanked off; the one which came to perfection contained 190 seeds, of which 52 were embryonated. I likewise tried the converse experiment, and placed pollen of the *T. pinnatistipula* on six flowers of the *T. mollissima*, and thus got three ovaries to set; one of these was entirely destitute of seeds, while the others conjointly yielded 116 seeds, but these were all small and imperfectly developed.

From the results of experiments in 1862, we have seen that the *Tacsonia pinnatistipula* could not be impregnated with its own pollen. Nevertheless, from the above favourable results with pollen of the *T. mollissima*, I determined to again test its impotence with its own pollen, which is known to be good when applied to another species. I accordingly fertilized ten flowers with own pollen; but the results simply confirmed those derived from previous experiments, as the ovaries of not even one swelled. With respect to the self-fertility of the *T. mollissima* the case is very different, as I have found it fruit freely when treated with own pollen, and, further, that these fruits yield an abundance of good embryonated seeds.

There is another point here worthy of a passing notice. In the above experiments on *Passiflora racemosa* as female, we have seen that this species is susceptible of fertilization by the pollen of *Tacsonia mollissima*. In the converse experiment, however, the results are different, the pollen of *P. racemosa* proving utterly

TABLE OF PURE AND MIXED UNIONS OF SPECIES OF *PASSIFLORA, DISEMMA,* AND *TACSONIA.*

	Total number of flowers fertilized.	Total number of ovaries produced.	No. of ovaries whichdropped prematurely.	Number of good ovaries.	Total number of seeds.	Number of apparently good seeds.
1. Passiflora racemosa by pollen of P. cærulea No. 3	8	3	3	...	.....	.....
2. Passiflora racemosa by pollen of P. cærulea No. 1	6	3	1	2	235	197
3. Passiflora cærulea No. 1 by pollen of P. racemosa	6	3	2	1	115	87
4. Passiflora racemosa by pollen of P. cærulea No. 2	8	0	...	...	.....	.....
5. Passiflora cærulea No. 2 by pollen of P. racemosa	3	1	...	1	105	68
6. Passiflora racemosa by pollen of Tacsonia mollissima	6	3	2	1	142	22
7. Tacsonia mollissima by pollen of Passiflora racemosa	6	0	...	...	.....	.....
8. Passiflora racemosa by pollen of P. alata No. 1	10	7	3	4	784	512
9. Passiflora alata No. 1 by pollen of P. racemosa	10	0	...	...	.....	.....
10. Passiflora racemosa by pollen of P. alata No. 3	6	3	2	1	158	114
11. Passiflora cærulea No. 1 by pollen of P. cærulea No. 2	4	2	2	...	.....	.....
12. Passiflora cærulea No. 2 by pollen of P. cærulea No. 1	4	3	2	1	154	143
13. Passiflora cærulea No. 1 by pollen of P. cærulea No. 3	4	3	1	2	243	237
14. Passiflora cærulea No. 2 by pollen of P. cærulea No. 3	4	3	...	3	293	262
15. Passiflora alata No. 1 by pollen of P. alata No. 2	8		1	3	674	560
16. Passiflora alata No. 2 by pollen of P. alata No. 1	4	...	...	...	.....	.....
17. Passiflora alata No. 1 by pollen of P. alata No. 3	6	2	2	...	.....	.....
18. Passiflora alata No. 3 by pollen of P. alata No. 1	4	1	1	...	.....	.....
19. Passiflora alata No. 1 by pollen of Disemma Adiantoides	6	...	...	...	.....	.....
20. Disemma Adiantoides by pollen of Passiflora alata No. 1	6	4	2	2	258	46
21. Disemma Adiantoides by own pollen	3	3	...	3	731	720
22. Disemma coccinea by pollen of Passiflora alata No. 1	6	2	1	1	74	12
23. Disemma coccinea by own pollen	3	3	...	3	596	586
24. Passiflora holosericea by pollen of P. manora	10	7	...	7	no seeds.	
25. Passiflora manora by pollen of P. holosericea	10	1	1	...	.....	.....
26. Tacsonia pinnatistipula by pollen of Tacsonia mollissima	6	3	2	1	190	52
27. Tacsonia mollissima by pollen of Tacsonia pinnatistipula	6	3	1	2	116	0
28. Passiflora racemosa by own pollen	20	1	1	...	.....	.....
29. Passiflora cærulea No. 1 by own pollen	12	...	...	...	.....	.....
30. Passiflora cærulea No. 2 by own pollen	8	...	...	...	.....	.....
31. Passiflora alata No. 1 by own pollen	20	...	...	...	.....	.....
32. Passiflora alata No. 2 by own pollen	12	...	...	...	.....	.....
33. Passiflora alata No. 3 by own pollen	12	...	...	...	.....	.....
34. Passiflora holosericea by own pollen	24	...	...	...	.....	.....
35. Passiflora manora by own pollen	18	...	...	...	.....	.....
36. Tacsonia pinnatistipula by own pollen	10	...	...	...	.....	.....
37. Tacsonia mollissima by own pollen	3	3	...	3	740	721

impotent on the stigmas of the *T. mollissima*, for not even one of the ovaries thus treated swelled.

For facility of reference, I will here subjoin, in a tabulated form, though in a somewhat different order, the more interesting results of the foregoing experiments.

Conclusion.—In the annexed Table we have the results of 37 distinct unions, in which 294 flowers were experimented upon, and the following curious phenomena are exhibited in the functional correlations of the sexual elements.

First, from ten unions of *Passiflora racemosa*—six unions as female and four as male—with other species, six fertile conjunctions were the result. Of these, one instance alone occurs in which the two species reciprocally fertilized each other, viz. in the case of *P. racemosa* and *P. cærulea* No. 1. With the two other plants of *P. cærulea* Nos. 1 & 2, *P. racemosa* treated as female yielded nothing, whereas by a converse experiment, *P. cærulea* No. 2 by pollen of *P. racemosa*, successful conjunctions were effected (*vide* Table, line 5). Again, *P. racemosa* may be readily fertilized by pollen of two individuals of the *P. alata* Nos. 1 & 3 (*vide* Table, lines 8 & 10), yet I failed in effecting a converse union by applying pollen of the *P. racemosa* to the *P. alata* No. 1. Similar results were derived from experiments on the *P. racemosa* and the *Tacsonia mollissima*, pollen of the latter proving potent on the stigmas of the former, whereas in the converse case the pollen of the *P. racemosa* is utterly ineffective on the stigmas of the *T. mollissima*. Though the *P. racemosa* will thus simply or reciprocally unite with the above species, it will be seen, by looking at line 28 of Table, that it is, nevertheless, perfectly sterile when treated with its own pollen. It is further worthy of remark that, with the exception of *T. mollissima*, the other five plants experimented upon likewise proved insusceptible of fertilization by their own pollen.

Secondly, in lines 11 to 14 inclusive of the Table we have the results of four unions in each case between three plants of the *P. cærulea*. These show that the pollen of an individual, A 1, for example, will readily fertilize the female element of another individual, A 2, whereas A 2 will not fertilize A 1; yet the female elements of both A 1 & 2 are susceptible of fertilization by the pollen of a third individual, A 3. Again, by consulting lines 29 & 30 of the Table, we see that the plants here given as A 1 & 2 cannot be fertilized by their own pollen, and I am told that plant A 3 is likewise insusceptible to fertilization by its own pollen.

Thirdly, we have the complicated results of the pure and mixed

unions of the three individual plants of the *P. alata* one with another, and with distinct species. Of the four pure unions given in lines 15 to 18 inclusive of the Table, one alone is fertile; thus the female element of A 1 can be fertilized by the male element of A 2, but the male element of the former fails to effect fertilization on the female element of the latter. Nearly similar results are afforded in the reciprocal experiments with A 1 and A 3, in which we have no fertile unions, though we have clearly symptoms of a conjunctive susceptibility in the setting of three of the ovaries (*vide* Table, lines 17 & 18). Again, the male elements of two of these plants of *P. alata*, A 1 & 2 respectively, fertilize the female element of the *P. racemosa*; and the male element of A 1 will fertilize two distinct species of the nearly allied genus *Disemma* (*vide* Table, lines 20 & 22). Though we have here proofs of the potency of the male element of these three plants of the *P. alata* and of the goodness of the female element of one of them, they nevertheless all proved utterly impregnable by their own pollen (*vide* Table, lines 31, 32 & 33).

Fourthly, we have the curious results of the unions between *P. holosericea* and *P. manora* (*vide* Table, lines 24 & 25), in which the male element of the latter effects the perfect development of the ovaries of the former, while it utterly fails in effecting the slightest development of the seeds. Again, in the converse experiment the male element of the *P. holosericea* is almost impotent on the female element of the *P. manora*, as only in one instance did a single ovary set, and this did not continue swelling. When these two species are fertilized with their own pollen we find utter impotence, as shown in lines 34 & 35 of the Table, for in a large number of flowers thus fertilized in no single instance did an ovary set.

Lastly, the male element of the *Tacsonia mollissima* effectively fertilizes the female element of the *T. pinnatistipula*, while in the converse experiment, though the pollen of the *T. pinnatistipula* applied to the stigmas of *T. mollissima* effects the perfect development of the ovarian coats and the hard or spermodermic coverings of the seed, it utterly fails in effecting the development of the embryo and albuminous matter. Again, *T. pinnatistipula*, though in general very insusceptible to own pollinic influence, does in rare cases, as shown in previous details, yield a fine plump ovary filled with apparently good seeds. On examination, however, I have invariably found that the spermoderm and albumen had alone been developed, while the embryo was entirely absent.