NEW OBSERVATIONS ON THE GENETICS OF PEAS (*PISUM SATIVUM*).

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(With Four Text-figures.)

These experiments relate to

(1) The origin and properties of two new varieties.

(2) The genetics of yellow pod, and of cotyledon colour.

(3) Two new linkage groups.

New Varieties.

Reduced stipules.

In the first variety the stipules are reduced (Fig. 2), being only a little larger than those of *Lathyrus*. It appeared spontaneously in 1915, as a single plant in a row of the variety Duke of Albany raised from seed obtained from Messrs Sutton. Messrs Sutton inform us that they have never observed a similar form. Seed from this plant gave 30 plants all with reduced stipules. Associated with the reduction in size of stipules a slight increase in size of leaflet was observed. In this family, among the green podded plants one was noticed as having *yellow pods*. A description of this and of its peculiar genetic behaviour will be given later (p. 128).

The form with reduced stipules was crossed with Duke of Albany type and rogue (Bateson and Pellew, 1915) giving F_1 normal, and F_2, 3 normal : 1 reduced stipules. Crosses were also made with various other types, especially with varieties having salmon-coloured flowers, and from these, F_2 families were grown showing linkage of the purple factor (B) with that for normal stipules (S). These families were all derived from the cross $Bs \times bS$, the reduced-stipuled strain being white carrying the B factor. The salmon flower colour was introduced from the fasciated form known as the "Mummy" Pea.

F_2 and comparable F_3 families from the cross Bs × bS.

	Coloured				Whites	
	BS	*bS*	*Bs*	*bs*	*S*	*s*
559—68. 21 ...	90	37	32	2	31 :	15
360—2. 22 ...	15	5	6	—	6 :	2
367—78. 22 ...	80	28	37	1	37 :	15
346—9. 22 ...	42	24	25	1	20 :	5
381. 22	9	4	4	—	none (F_3)	
511—2. 21 ...	13	7	2	—	10	1
Observed numbers	249	105	106	4	104	38
Calculated numbers	*241·5*	*106·5*	*106·5*	*9·5*		

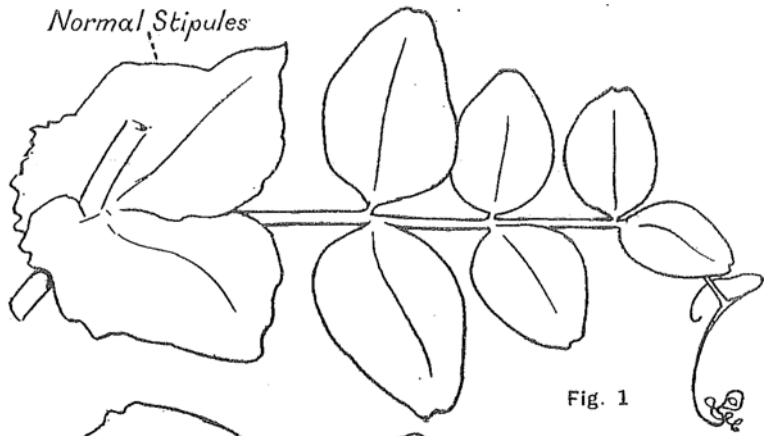

Fig. 1

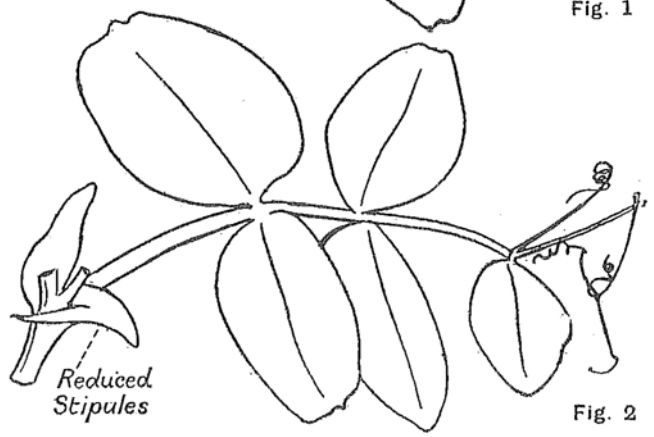

Fig. 2

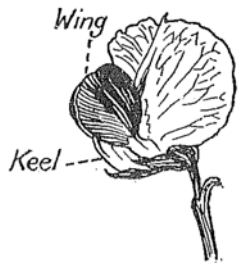

Fig. 3

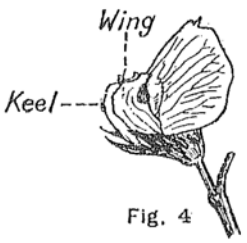

Fig. 4

The calculated numbers represent a gametic series of

$$1\ BS : 2{\cdot}5\ Bs : 2{\cdot}5\ bS : 1\ bs,$$

the cross-over classes being about 28 %.

Other allelomorphs with which *S* is not linked are as follows:

Linked with each other { Round—wrinkled cotyledons.
Tendrilled—acacia leaves.

Tall—dwarf.

Colour—white.

Normal habit—fasciated habit.

Yellow—green cotyledons.

Glaucous—emerald (free seeds).

Linked with each other { Glaucous—emerald ("chenille").
Normal wings—keeled wings.

Keeled Wings.

The peculiarity of this form (Fig. 4) is that the wings have undergone homoeosis, being transformed into the likeness of the keel. Each wing stands in its normal place as a separate petal, but the tissue of which it is composed is in colour and structure exactly like the keel, being thrown up into longitudinal ridges like those of the normal keel. The rest of the flower is normal.

This form was shown to us by Mr W. A. Giles (of Messrs Sutton) in 1919. It had first been noticed (? in F_3) among the descendants of a cross between a vetch-like rogue in Pride of the Market (a dwarf round-seeded variety) and the Mummy Pea (salmon bicolor). Keeled wings were combined with numerous characters introduced in the original cross, and several of these forms were given to us by Messrs Sutton. Since in keeled wing flowers on coloured plants the transformed wings have only the small amount of pigment characteristic of normal keels, they are not easily referred to their colour types.

Linkage of normal-keeled wing with glaucous-emerald has been tested only in the cross glaucous, keeled × emerald, winged. The normal-winged emerald used in these crosses was the "chenille" type (*i.e.* seeds cohering when ripe) investigated by Vilmorin (1911), and Meunissier (1922)[1].

[1] Vilmorin proved the existence of two distinct kinds of emerald, for from the cross emerald "chenille" by emerald free seeds var. "Emereva," came a glaucous F_1, and in F_2 glaucous and emerald in the ratio 9 : 7. We have also observed a glaucous F_1 from emerald "chenille" × emerald free seeds. From the results of this cross and from the cross glaucous free seeds × emerald "chenille" Vilmorin showed that glaucous segregates are predominantly free seeded, and emerald segregates "chenille," but that the "chenille" character

Tabulated below are two F_2 and six F_3 families (pooled) from a cross between emerald-chenille normal wings and glaucous free keeled wings. K = normal as opposed to k, keeled wings, G = glaucous as opposed to g, emerald.

Families from $Kg \times kG$.

		KG	Kg	kG	kg
F_2. 35—1. 22	...	48	31	25	1
,, 522—9. 21	...	212	82	98	3
F_3. 385—90. 22	...	114	51	51	1
Observed numbers	...	374	164	174	5
Calculated numbers	...	*365·7*	*172*	*172*	*7·2*

The calculated numbers represent a gametic series of

$$1\,KG : 4\,Kg : 4\,kG : 1\,kg,$$

the cross-over classes being 20 %.

Other allelomorphs with which K is not linked are:

Linked with each other { Round—wrinkled seeds. / Tendrilled—acacia leaves.

Tall—dwarf.

Normal—fasciated habit.

Colour—white.

Yellow—green cotyledons.

Linked with each other { Purple—salmon. / Normal stipules—reduced stipules.

The linkage groups in *Pisum* of which there is now evidence are therefore three, the two here reported besides that between tendrilled—acacia and round—wrinkled seed. The other linkages which have been supposed to exist are not in our opinion authenticated. The haploid chromosome number is 7.

Yellow Pods and Cotyledon-colour.

We have mentioned (p. 125) that in the family raised from our original plant with reduced stipules, a plant was noticed having yellow pods. From this plant has been raised a strain breeding true to yellow pod.

is much influenced by other characters (*e.g.* colour) and also by climatic conditions. These observations have been interpreted by O. White 1917 as indicating linkage between the two characters, but after further investigations Meunissier concludes that the "chenille" character "*est toujours corrélatif du caractère émeraude.*" Our own records of "chenille" in relation to glaucous-emerald are very limited and inconclusive. As far as we know, no case is known of plants of the cross-over combinations breeding true, and linkage of these characters remains unproven.

Subsequently we noticed that the cotyledons and testa of this particular strain are always pale yellow[1]. Yellowing of the pods and stems occurs during the ripening stages, the straw being creamy-yellow. This distinction is very striking under ordinary conditions, though in a wet summer the colour change is much less definite, and the plants become discoloured by moulds, so that discrimination between green and yellow pod plants is difficult and counts of mixed families are unreliable. The plants are also very slightly paler, both in stem and foliage, than the related green-podded strain even in earlier stages of growth.

The genetic behaviour of yellow pod forms has been investigated by Mendel and Tschermak (1904, p. 11). Mendel described the variety he worked with as having pods "vividly yellow, in which colouring the stalks, leaf-veins, and calyx participated." He found that this group of effects behaved as a simple recessive to green. Tschermak confirmed this result working with a variety of Sugar Pea with yellow pods.

Recent work with yellow pods has led to an extension of our knowledge of the genetics of cotyledon colour. Yellow and green, round and wrinkled, are of course the most familiar of all Mendelian characters, having been studied on an extensive scale, and ample evidence of their independence exists. O. White, however, in 1916 published observations which, as he interpreted them, suggested a definite linkage between round and a peculiar "yellow" which behaved as a recessive. In that paper he does not allude to the fact, nevertheless incidentally mentioned in his later report (1917, p. 567), that the variety used by him had yellow pods. As will subsequently appear, the suggestion of linkage is an illusion caused by the special phenomena peculiar to the yellow pod variety. As this variety is otherwise under consideration in this paper, we venture to include a preliminary note on our observations of its seed-characters though the investigation is still incomplete.

Our yellow-podded variety has wrinkled seeds. Their cotyledon colour is a *pale yellow*. This colour is not so full as that of the ordinary yellow-seeded varieties commonly used by geneticists. But in looking over samples of truly yellow-seeded peas, seeds may often occur, which could not readily be distinguished by their colour from those here under consideration. Understanding of what follows will be facilitated if we here give an outline of the results arrived at.

The pale colour characteristic of our yellow-podded variety is recessive to ordinary green cotyledons as White found in his variety. If the

[1] Another yellow podded plant with yellow cotyledons appeared in a crop of Duke of Albany in 1911. This plant bred true to type. We did not keep the strain.

green-seeded variety used be a *wrinkled* (as our pale seeds also are), green is dominant, and an ordinary F_2 ratio, 3 greens : 1 pale follows the pales being those which would become yellow-podded plants. But if *round*-seeded varieties are used in the cross, there is a complication from the fact that the introduction of the round character may have a direct effect on the colour of the seeds.

The simplest cross of that kind has not been made by us, but it was made by White, who found that pale wrinkled × green round gives green round dominant. The details for F_2 are not given, but the classes were three only, the *pale round* class being missing.

We crossed the pale wrinkled with an ordinary round, *yellow*-seeded variety, Mummy, which gave round yellow F_1, and in F_2, three classes not further distinguishable on inspection, "yellow" round, green round, and "yellow" wrinkled[1]. At first sight, since green rounds are present, one expects *green wrinkled* also, but that class is missing.

The two sets of results are obviously reconcilable if it can be supposed that the absence of *pale round* in White's experiment and the absence of *green wrinkled* in ours are both consequences of an influence of the roundness, such that the pale when round may be green. When a *wrinkled* green is used the results are normal, as we have seen.

The subsequent investigation is rendered difficult by the impossibility of distinguishing by eye the pale seeds from the yellows. Conversely there is often difficulty in distinguishing the pale seeds from greens, a difficulty which is especially met with in certain crosses. Green seeds are in many ordinary green varieties very liable to bleach, and this is notably the case with Duke of Albany. From our experience with this variety we incline to think that there is great difference in the individual plants of such sorts, and we expect that it would be possible to separate non-bleaching from bleaching strains in them. The "pale" seeds are probably a form in which the same liability to bleach exists in a higher degree. Exceptionally, wrinkled seeds from matings with the yellow-podded variety have come green when fresh, though only pale were expected, but we have noticed that in one case such seeds have bleached to the pale colour after being put away for a year.

Of the green or greenish round seeds in F_2 from the cross between Mummy and the yellow-pod variety, the majority have given plants with yellow pods. Strictly according to expectation all should have

[1] Mummy (seeds yellow round) × any green-podded (seeds green wrinkled) variety gives in F_2 an ordinary 9 : 3 : 3 : 1 ratio in seed-characters.

done this, but we have no difficulty in attributing the few exceptions to the impossibility of correctly sorting such material.

It must be clearly understood that the colour of the seeds does not, as we first thought possible, depend in any way directly on the colour of the maternal pods. Any mixture may occur in pods of either colour, if the appropriate parents are used. Whether it is possible to combine ordinary *dominant yellow* seeds with yellow pods as a true-breeding form we do not know, but we incline to think that this is not possible, and that the yellow pods and the pale colour of the cotyledons are due to the absence of a single factor. There is nevertheless some reason for supposing that a complex interrelation may exist between the colours of the testa and the degree to which the pale seeds assume their proper colour.

Until we know for certain that true yellows cannot be combined with yellow pods in a pure type, a factorial representation of the way in which the several forms are interrelated can only be conjectural. We are disposed however to regard the facts as pointing to the existence of a triple allelomorphic series composed as follows: (*a*) true dominant yellow cotyledons associated with green pods; (*b*) green cotyledons also associated with green pods; (*c*) pale cotyledons associated with yellow pods; the three standing in a descending order. As stated above, when the factor for round seed is associated with the lowest term in the series, the seeds which if wrinkled would have been pale, are often green or greenish.

Miss de Winton has given much help with the observations here recorded.

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