GENETICS AND CHEMISTRY OF FLOWER COLOUR VARIATION IN *LATHYRUS ODORATUS*

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(With Plate XIV)

CONTENTS

1. Introduction

The genetics of flower colour variation in the Sweet Pea has been investigated by Punnett and others, who have described some eleven factors (see Punnett, 1925, 1932, 1936). The chemistry of the anthocyanins which are responsible for the variations in colour has been elucidated by Robinson & Robinson (1931, 1933, 1934), who have identified the pigments of a number of varieties. As part of a comparative investigation of flower colour in a number of plants, the late L. H. A. Stone in 1932 initiated a combined genetical and chemical study of *Lathyrus odoratus*. Some of the results have been noted by Scott-Moncrieff (1936) in her survey of the subject; but it is now possible to give a more complete account, embracing practically the whole range of flower colour.

Haldane (1935, 1937) has indicated the contributions which it was hoped this type of work would make towards the solution of some fundamental problems of genetics and physiology. We may here mention the following: First, a knowledge of the chemical nature of the differences between any two genotypes is clearly very helpful when considering homologous variations in different species and genera; comparisons between species can be made much more precisely. Secondly, where the chemical difference between two genotypes differing by only a single factor is a very simple qualitative one, it may be regarded as a more or less direct expression of the activity of a particular gene. Finally, it is possible that some information concerning the mode of synthesis of the flower pigments may be derived from a study of their inheritance.

The system of genetical symbols used in this paper is that adopted by Scott-Moncrieff (1936). For convenience, a list of factors is given below, in both the Punnett (1923) and the Scott-Moncrieff conventions:

Recessive factor	Punnett symbol	Scott-Moncrieff symbol
Red	a_1	e
Hooded	a_2	h
Maroon	b_4	m
Dull	d_2	d
r-white	f_1	r
Marbled	f_3	r′
c-white	g_1	c
Flake	g'_1	c′
Copper	g_2	k
Mauve	g_3	co
Dark wing	—	dw

2. Methods

(*a*) *Genetical*

Owing to extensive pollination by bees, we have found it necessary to protect all flowers required for selfing by means of waterproof paper bags perforated with holes about 3 mm. in diameter. The pods develop satisfactorily inside the bags.

(*b*) *Chemical*

The chemical testing was done by methods already described (Robinson & Robinson, 1931, 1932, 1933) which need not be considered here. The *p*H determinations were made by taking a certain number of flowers (usually six), detaching and grinding the standards and wings, adding a small quantity of distilled water, and measuring the *p*H of the extracted sap by means of a glass electrode apparatus. In this way it was possible to compare the extracts from different flowers. The *p*H measurements

were mostly made by Miss V. C. Sturgess, to whom we wish to express our thanks. The leucoanthocyanins were extracted by boiling the testas (previously removed from the seeds after softening with methyl alcohol and hydrochloric acid) with 1% hydrochloric acid. The colourless solution so obtained was then boiled with an equal volume of concentrated hydrochloric acid in order to convert the leucoanthocyanins into anthocyanidins.

3. Inheritance of two new factors

(*a*) *Purple-salmon*

Data on the inheritance of the factor "salmon" (**sm**), which occurs in numerous modern varieties (e.g. "Ascot", "Beatall", etc.), are presented in Tables I–IV. The effect on flower colour, as will be seen from Pl. XIV, is to make it more orange and somewhat paler. [In the very pale types it is difficult to distinguish salmon from red.] Salmon is completely recessive to the purple wild type, and hypostatic to the factor red (**e**), i.e. salmon flowers can only be produced in the absence of both factors **e** and **Sm**. Table I shows the segregation of the three colours

TABLE I

F_2 from purple × salmon (F_1 purple)

Ref. no	Purple (**E Sm** + **E sm**)	Red (**e Sm**)	Salmon (**e sm**)
57/38	51	16	3
58/38	76	15	11
Total	127	31	14
(Calc. 12:3:1	129·00	32·25	10·75)

χ^2 on totals = 1·06. $P_{[2]}$* = 0·70–0·50.

* Small no. in brackets = no. of degrees of freedom.

purple, red and salmon in an F_2 derived from a cross between purple and salmon. There is no significant deviation from the 12:3:1 ratio expected on the hypothesis.

It was at first thought that **sm** was allelomorphic to **e**, since on crossing salmon with certain purple strains (e.g. the mauve variety "Chieftain") only salmon and purple types were obtained in the F_2, and no reds. Crossing a salmon with a red gave a red F_1 and in the F_2 red and salmon in the ratio 3:1 (see Table III). But it was later discovered that the variety "Chieftain" contained **sm**, and it did not show phenotypically on account of the epistasy of **E**. Crossing "Chieftain" with red produced a purple F_1 and all three types in F_2, the ratios not differing significantly from 12:3:1 for purple:red:salmon (see Table IV).

The genetical constitutions of the three types of flower colour may therefore be given as follows: (*a*) purple, **E Sm** or **E sm**; (*b*) red, **e Sm**; and (*c*) salmon, **e sm**, the two kinds of purple being distinguishable only by their breeding behaviour.

TABLE II

F_2 from "Chieftain" (pale purple) × salmon (F_1 purple)

Ref. no.	Purple (including mauve)	Salmon (including pale salmon)
59/38	33	9
60/38	21	6
61/38	28	10
62/38	39	17
63/36	68	15
64/36	55	17
Total	244	74
(Calc. on 3:1	238·5	79·5)

χ^2 on totals = 0·51. $P_{[1]} = 0{\cdot}5–0{\cdot}3$.

TABLE III

F_2 from red × salmon (F_1 red)

Ref. no.	Red	Salmon
67/38	24	10
68/36	16	6
Total	40	16
(Calc. 3:1	42	14)

χ^2 on totals = 0·38. $P_{[1]} = 0{\cdot}5–0{\cdot}7$.

TABLE IV

F_2 from "Chieftain" × red (F_1 purple)

Ref. no.	Purple	Red	Salmon
71/38	42	12	6
73/38	33	5	2
Total	75	17	8
(Calc. 12:3:1	75·00	18·75	6·25)

χ^2 on totals = 0·65. $P_{[2]} = 0{\cdot}8–0{\cdot}7$.

(b) Normal-bright

Data on the inheritance of the factor "bright" (**br**), which occurs in many modern varieties (e.g. "Beatall"), are given in Table V. The effect on the flower colour is to deepen and redden it. The expression of the factor is only observable at all clearly in those types which are pale, e.g. those containing the factor mauve (**co**) and among these the red and salmon types show the effect most markedly. Evidently the more intense colours cannot well be further intensified.

From Table V it will be seen that bright is inherited as a simple mendelian factor. It is not completely recessive to the normal, though the heterozygotes cannot be distinguished from the dominant homozygotes with absolute certainty. It is worth noting here that of the twenty-four mutants so far described in the sweet pea, only three (acacia, bright and flake-modifier) are not completely recessive to their wild-type allelomorphs, and of these three only acacia has any marked effect

TABLE V

F_2 from normal × bright (all mauve)

	Ref. no.	Normal	Bright
	61/38	28	10
	62/38	39	17
	71/38	41	11
	74/38	22	7
Total		130	45
(Calc.	3:1	131·25	43·75)

χ^2 on totals = 0·047. $P_{[1]} = 0{\cdot}8$–$0{\cdot}9$.

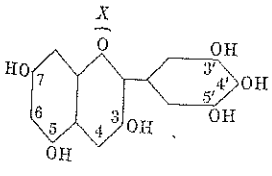
when no other recessive factors are present. Bright can only be distinguished on mauve (co) forms, and flake-modifier on flaked (c′) forms. Evidently there is some correlation between the complete recessiveness of a mutant and the necessity for it to occur simultaneously with another non-wild-type factor in order to produce a visible effect.

As regards linkage, the factor bright is very closely linked with light-axil (l) in the *B* chromosome of Punnett.

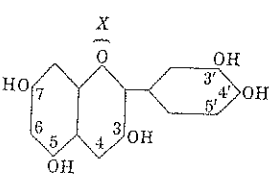
4. Description of chemical differences between various genotypes

(a) *Variation in state of oxidation of anthocyanin molecule (factors* e, sm)

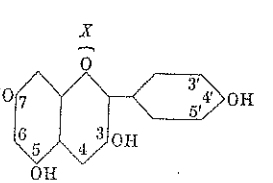
The purple sweet peas contain anthocyanins based on delphinidin (or its methylated derivatives petunidin and malvidin, or mixtures); the red flowers contain anthocyanins based on cyanidin (or its methylated derivative peonidin), and the salmon flowers pelargonidin. The formulae for the main anthocyanidins are given below:



Delphinidin (purple)



Cyanidin (red)



Pelargonidin (salmon)

It will be at once evident that the factor **e** (red) is associated with the loss of a single hydroxyl group at the 3′ position when the dominant allelomorph of salmon is present, and with the loss of two hydroxyl groups (at 3′ and 5′) when the recessive allelomorph of salmon is present. Similarly the factor **sm** (salmon) is associated with the loss of a single hydroxyl group at the 5′ position when the recessive allelomorph of red is present. When the dominant allelomorph of red is present, the factor **sm** has no effect on the phenotype. (When the anthocyanins are methylated, read methoxyl for hydroxyl in the above.) Therefore the factors **e** and **sm** can be considered to control the state of oxidation of the anthocyanin molecule.

In the sweet pea the distinction between delphinidin and cyanidin types is usually sharp, with no mixtures of the two pigments, though in the red variety "Miss Hunt" there is a trace of a malvidin derivative, and in the purple variety "Purple Invincible" a trace of cyanidin derivative. So far as is known, the anthocyanins of salmon flowers are derived from pelargonidin only, without admixture of other types, though it would be difficult to detect small amounts of peonidin in the presence of pelargonidin.

Apart from these qualitative differences, it is possible that there are differences in the concentration of pigment in the three types, since the red varieties are rather paler than the corresponding purples, and the salmons paler than the reds. It is however very difficult to make a quantitative comparison between different pigments.

(*b*) *Variation in p*H *of cell sap* (*factor* **d**)

The recessive factor dull (**d**) has been described by Punnett (1925). All types containing the factor (e.g. the varieties "Lord Nelson", "Violet Queen", etc.) are markedly bluer, both in standard and wings, than the corresponding **D** types. There are no differences whatever in the anthocyanin pigments in the two types, nor any marked variation in co-pigment. A test for *p*H differences was made, taking a series of pairs of genotypes, each pair being genetically identical in all known flower colour factors except **d**. It was therefore possible to consider the effect of the factor **d** in different genetic environments. The members of each pair were tested at the same time, reducing environmental fluctuations to a minimum. The *p*H measurements are given in Table VI.

The dull type was found always to give a more alkaline extract than the corresponding normal type, the difference between the means being

about 0·6 of a *p*H unit. "Student's" *t* test was carried out, and the difference between the two means shown to be highly significant.

Clearly therefore the blueing effect of **d** is to be attributed to its action in raising the *p*H of the cell sap.

(*Note.* It was formerly thought that the factor dull was associated with a difference in the amount of methylation of the anthocyanin (see Scott-Moncrieff, 1936). This is now known to be erroneous.)

TABLE VI

*p*H *of extracted sap from various genotypes containing* **D** *and* **d**

"Genetic background"	**D**	**d**
Purple (+)	5·22	5·97
Copper (**k**)	5·18	5·77
Red maroon (**e m**)	5·22	5·90
Mauve (**co**)	5·05	5·88
Flake (**c′**)	5·78	6·04
Picotee (**p**)	5·56	5·86
Mean	5·34	5·93

$t = 4{\cdot}77$. $P_{[10]} < 0{\cdot}01$.

(c) *Variation in quantity of anthocyanin and anthoxanthin*

(i) *Dark wing* (**dw**). The purple wild sweet pea has the wings much paler and bluer than the standard. All cultivated forms known to us except "Purple Invincible" and "Painted Lady" contain **dw**, which reddens and intensifies the colour of the wings, leaving the standard unaltered (see Bateson *et al.* 1906). Even dark wings are somewhat bluer than the standard (Pl. XIV, fig. 7).

Dark wings differ chemically from light in having more anthocyanin but less anthoxanthin co-pigment. The increase of anthocyanin is responsible for the intensification, and the diminution of co-pigment for the reddening effect.

(ii) *Copper* (**k**).

(iii) *Maroon* (**m**). The recessive factors copper (formerly "red-purple") and maroon have been described by Punnett (1922 and 1923 respectively) who showed them to be genetically distinct. Maroon occurs in many modern varieties (salmons, crimsons, maroons) but copper only in experimental material. In appearance the two types are extremely similar; in both, the wings are so much reddened that they are of exactly the same tint as the standard. Both types are particularly prone to bleaching in the sun. The reddening and tendency to bleaching are associated with a complete suppression of co-pigment.

Interactions between **k** or **m** and **dw** are such that **dw** has only an

intensifying effect on the anthocyanin in the wings in **k** or **m** types, and no reddening effect. Since there is no co-pigment in **k** or **m** types, no further reduction can be brought about by **dw**.

(iv) *Mauve* (**co**). This factor, occurring in many modern varieties (e.g. "Chieftain", "Beatall", etc.), has been described by Punnett (1932). As compared with the dominant purple form, "mauve" flowers are paler and bluer. They contain less anthocyanin, but much more co-pigment, both in standard and wings, than purple forms.

co interacts with **dw** in the following manner. In **Co** forms, as mentioned above, the effect of **dw** is to intensify and redden the wings. In **co** forms, not only the wings but also the standard is reddened. This is to be expected when one considers that **Co** forms have no co-pigment in the standard, and therefore none to be suppressed by **dw**. When there is co-pigment in the standard, as in **co** forms, **dw** can inhibit it there as well as in the wings.

The factors for mauve on the one hand and for copper or maroon on the other have contrary effects: the first is associated with an excess, the second and third with a lack of co-pigment. It is therefore interesting to see what would be the effect of mauve and the others in combination. When mauve and maroon were combined, the double recessive was found to be as pale as mauve, but much redder. On testing, it was found to have practically no co-pigment. Therefore, when **m** (maroon) is present, **co** only has a diluting effect on the anthocyanin, and no influence on the production of co-pigment.

(v) *Bright* (**br**). This factor, as described above intensifies and reddens the colour of mauve flowers, but has no marked effect on **Co** types. The chemical effect of bright is to increase the amount of anthocyanin and decrease the amount of co-pigment, i.e. the opposite effect to mauve. Bright mauves are intermediate between normal mauve and purple, though nearer to the latter than the former. Hence **br** does not quite compensate for **co**.

(vi) *Picotee* (**p**). This factor (see Bateson *et al.* 1904, p. 87) is similar to mauve, but more extreme—there is only a tinge of colour left in the flower. Picotees contain a very large amount of co-pigment.

(vii) *Hooded* (**h**). This factor, which occurs in all modern varieties, was originally described by its effect on the flower shape, but the colour is also modified (Bateson *et al.* 1908, p. 7). In hooded forms the standard and wings are almost identical in tint (though not necessarily in intensity), the standard being bluer and the wings a little redder than in the wild type. This is brought about by the production of some co-pigment in the

standard, which normally contains none, and a slight reduction in the amount of co-pigment in the wings.

The interactions between hooded and other factors are complex and so far not worked out. With copper or maroon types, however, there is no difference at all between **H** and **h** as regards flower colour. Apparently the suppression of co-pigment by **k** or **m** is sufficiently strong to prevent any variations in co-pigment being brought about by **h**.

(viii) *Other factors.* Besides the factors described above, there are several others which dilute or inhibit anthocyanin in the flowers. The chief of these are as follows: **c**-white, **r**-white, **c′** = flaked, **r′** = marbled (Punnett, 1925, 1936) and two undescribed factors ("tinged" and "Silver lining" (Beale, unpublished)). In all these types so far as they have been tested there is some anthoxanthin, which never appears to be suppressed by the same factors as the anthocyanin. This is to be contrasted with the factors **y** in *Antirrhinum majus* and $\mathbf{c_a}$ in *Pharbitis nil*, which simultaneously suppress anthocyanin and anthoxanthin (Scott-Moncrieff, 1936). We have not yet obtained the double recessive types containing **c** together with **m** or **k**.

(*d*) *Variation in proportions of methylated and unmethylated anthocyanins*

As already mentioned (p. 380), the anthocyanins in the sweet pea may or may not be methylated. Hitherto we have not succeeded in associating any particular genetic factor with the degree of methylation, but it is interesting to note a correlation between co-pigmentation and methylation, i.e. those forms which have a large amount of co-pigment (such as co-types) contain pure methylated pigments such as malvidin or peonidin derivatives, while unco-pigmented types such as copper and maroon contain an appreciable admixture of unmethylated anthocyanin. This does not apply of course to the salmon (pelargonidin) types, since an anthocyanin with the 4′ hydroxyl methylated has never been found in nature.

(*e*) *Glycosidal differences*

While the older varieties contained usually pure 3:5-dimonoside types, the modern bright salmon sweet peas sometimes contain a proportion of a pigment having a high distribution in amyl alcohol. No genetical data on this point are available, but there is evidently no similarity with the inheritance of glycosidal differences in *Callistemma chinensis* (Wit, 1937) and *Verbena* (Beale & Scott-Moncrieff, unpub-

lished), where a single factor may control the difference between pure dimonoside and pure monoside.

(*f*) *Leucoanthocyanins*

Robinson & Robinson (1933) have given a preliminary account of the leucoanthocyanin from sweet pea seeds. The position at the moment is as follows: (1) seeds from salmon flowers give a leucoanthocyanin yielding pelargonidin (or possibly peonidin), (2) seeds from red flowers give a leucoanthocyanin yielding cyanidin, and (3) seeds from purple flowers give a leucoanthocyanidin yielding delphinidin with some cyanidin.

Seeds from white flowers have given a leucoanthocyanin corresponding to cyanidin, but the genetical constitution of these seeds as regards **e** (red) and **sm** (salmon) was unknown. It is worth noting that **c**-white seeds are a pale brown colour, as compared with the almost black colour of the normal **C** types. Hence though **c** is associated with a diminution of brown pigment in the testas, the amount of leucoanthocyanin is apparently unaffected.

5. Discussion

The inheritance of the various flower colour types and their pigments in *Lathyrus* may now be compared with that of homologous variations in other plants. Consider first **e** and **sm**. In general, the factors associated with the more oxidized anthocyanins are almost always dominant to those associated with the less oxidized anthocyanins (see Scott-Moncrieff, 1936). Our factors clearly fit in with this scheme. So far only two other plants with all three types of anthocyanin (i.e. those derived from delphinidin, cyanidin and pelargonidin) have been investigated: these are *Streptocarpus* (Lawrence *et al.* 1939) and *Callistemma chinensis* (Wit, 1937). The position in *Streptocarpus* is identical with that in *Lathyrus*, the factors **o** and **r** corresponding to **e** and **sm** respectively. In *Callistemma* there are also two recessive factors, but there is some evidence that they are not independent, as in *Streptocarpus* and *Lathyrus*, but allelomorphic (**R**–**r′**–**r**, corresponding to delphinidin, cyanidin and pelargonidin).

A consideration of the biochemical significance of the epistasy of the red over the salmon factors in *Lathyrus* (and of the corresponding factors in *Streptocarpus*) may be left over until further data from other plants

are forthcoming, and until it can be seen whether or not this epistasy is a constant feature.

Consider second the factor **d** affecting the acidity of the cell sap. Corresponding factors in other plants are as follows: in *Primula sinensis* **r**, in *P. acaulis* **s**, in *Papaver Rhoeas* **p** (Scott-Moncrieff, 1936) and in *Trifolium pratense* $\mathbf{c_b}$ (Price & Williams, unpublished). In all of these the alkaline form, as in *Lathyrus odoratus*, is recessive.

The third main kind of flower colour variation in *Lathyrus*, namely variation in the amount of co-pigment, cannot be compared at all precisely with genetically determined co-pigment differences in other plants, because of the complexity of the situation in *Lathyrus* itself, where there are at least seven factors (dark wing, hooded, copper, maroon, mauve, bright and picotee) concerned with the quantity of anthoxanthin and anthocyanin. These factors may be classified in the following manner: (*a*) mauve and picotee simultaneously reduce the amount of anthocyanin and increase the amount of anthoxanthin, (*b*) dark wing and bright increase the amount of anthocyanin and decrease the amount of anthoxanthin, and (*c*) copper and maroon suppress all anthoxanthin without affecting the amount of anthocyanin. The evidence of the first two of these classes supports the view of Lawrence & Scott-Moncrieff (1935) that there is a balance between anthocyanin and anthoxanthin production, and that increasing one leads to a decrease in the other as a consequence of a limitation in amount of a hypothetical precursor common to both. Such a precursor has been suggested by Robinson (1934). It will be interesting to determine how frequently examples of class (*c*) (specific suppressors of anthoxanthin) occur, and whether there are any examples of specific suppressors of anthocyanin. Further investigation of these problems is required.

Since anthocyanins and anthoxanthins have a rather similar chemical structure it might be supposed that factors affecting the state of oxidation of one would bring about a similar change in the other. This, however, is not so. Further evidence that this supposition is false is provided by the sweet pea; for the anthoxanthins in highly pigmented (**co**) types were found to be the same, namely the flavonols quercetin and kaempferol (only a trace of the latter) no matter whether the anthocyanin present was of the delphinidin, cyanidin or pelargonidin type.

Variation in co-pigmentation is evidently the most common way of changing the colour of sweet pea flowers. This may mean that the genes controlling such variation have a higher mutation rate than those concerned with other changes; or it may be merely that there are more ways

of varying the relative quantities of anthoxanthin and anthocyanin than of altering the structure of the anthocyanin molecule or the *p*H of the cell sap.

As contrasted with the entirely independent variation in degree of oxidation of anthoxanthin and anthocyanin, the leucoanthocyanins which occur in the seed coats show a correlated variation with the anthocyanins in the flowers. Evidently, leucoanthocyanins and anthocyanins are similar in their reaction to **e** and **sm**. This is interesting in view of the chemical relationship between anthocyanins and leucoanthocyanins (Robinson & Robinson, 1935).

In conclusion it may be stated that a genetical and chemical analysis of *L. odoratus* shows it to accord admirably with the majority of other plants which have been investigated in a similar way. In this connexion it is perhaps important to recall the fact that all variations which occur in the modern sweet peas have most likely arisen as mutations from a single wild form (similar to the variety "Purple Invincible"), introduced into England in 1699. The red "Painted Lady", the first cyanidin type, appeared in 1731, and the first "scarlet" (presumed pelargonidin) in 1793. Interspecific hybridization, which succeeds only rarely within the genus *Lathyrus* (see Senn, 1938), has apparently not been involved.

Summary

1. The inheritance of two new flower colour factors—bright and salmon—is described. Bright is an incomplete recessive, and salmon a recessive factor hypostatic to red (**e**).

2. Two factors, red (**e**) and salmon (**sm**), are associated with a difference in the degree of oxidation of the anthocyanins in the flowers, and with a similar difference in the leucoanthocyanins in the seed coats.

3. One factor, dull (**d**), is associated with a difference of *p*H in the cell sap of the flowers.

4. At least seven factors—dark wing (**dw**), copper (**k**), maroon (**m**), mauve (**co**); bright (**br**), picotee (**p**) and hooded (**h**)—are associated with differences in the relative amounts of anthocyanin and anthoxanthin co-pigment.

5. Variation in methylation of the anthocyanin is correlated with the quantity of anthoxanthin.

6. Variation in glycosidal residues has not so far been associated with any genetic factor.

7. *Lathyrus odoratus* agrees very closely with plants of other genera in regard to the inheritance of comparable chemical differences.

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EXPLANATION OF PLATE XIV

From paintings by H. C. Osterstock

Fig. 1. Purple, hooded, dark wing (delphinidin type), **h dw**.
Fig. 2. Red, hooded, dark wing (cyanidin type), **e h dw**.
Fig. 3. Salmon, hooded, dark wing (pelargonidin type), **sm e h dw**.
Fig. 4. Purple, light wing (much co-pigment and little anthocyanin in wings).
Fig. 5. Copper or maroon, dark wing (no co-pigment), **m** (or **k**) **dw**.
Fig. 6. Mauve, hooded, dark wing (much co-pigment and little anthocyanin), **co h dw**.
Fig. 7. Purple, dark wing (lower *p*H), **dw** (cf. fig. 4).
Fig. 8. Dull, dark wing (higher *p*H), **dw d**.
Fig. 9. Red, dark wing (lower *p*H), **dw e**.
Fig. 10. Dull red, dark wing (higher *p*H), **dw e d**.

Note. For differences between anthocyanidin types compare 1, 2 and 3; for differences of *p*H compare 7 and 8 with 9 and 10 respectively, and for differences in co-pigmentation compare 1, 4, 5, 6 and 7.