PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 1939 **230**, 149-178
doi: 10.1098/rstb.1939.0006

THE DISTRIBUTION OF ANTHOCYANINS IN FLOWERS, FRUITS AND LEAVES

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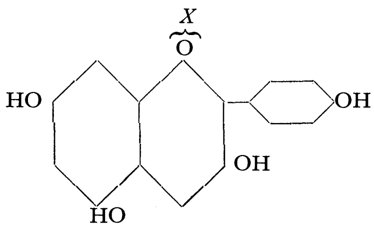
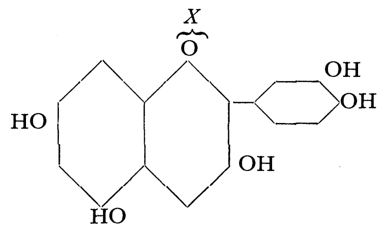
(*Received* 31 *October* 1938)

A series of papers has been published which are concerned with the investigation of the nature of the anthocyanins present in a variety of plants and in various organs, including flowers, fruits and leaves (Robinson and Robinson 1931, 1932*a*, 1933, 1934; Lawrence, Price, Robinson and Robinson 1938; Price and Sturgess 1938). The methods employed served to identify the fundamental anthocyanidins and in most cases the sugar type of the anthocyanins, but the sugars themselves were not identified. Thus glucoside is a term that includes galactoside in the sequel. The large number examined appears to justify a general review of the results, and in our opinion certain inferences may be drawn from the observed distribution of the anthocyanin types. In the first place, we find support for the view (Robinson 1934, 1936) that cyanidin is to be regarded as biogenetically the simplest of the three main classes, based respectively on pelargonidin (I), cyanidin (II) and delphinidin (III). On the supposition that the anthocyanins and other related substances (anthoxanthins, leuco-anthocyanins and catechins) are built up from simple carbohydrates through a series of aldol condensations, the hypothetical intermediate (IV) has been suggested as a basis from which all these compounds may be derived. This intermediate can be constructed from two hexose units and one triose, and is in the same state of oxidation as a carbohydrate. A mechanism of aldol condensations affords a natural explanation of the different state of oxidation of the two benzene nuclei because the component functioning as a carbonyl compound is reduced whilst the keto-methylene component is unaltered in state of oxidation in an aldol condensation. Hence the spear-head component is identified with the unfused aromatic nucleus and this should give $C_6 . C_3$ substances in the first place. These $C_6 . C_3$ compounds are known and are characterized by orientation of hydroxyl groups similar to those obtaining in the unfused benzene ring of the anthocyanins. The central three-carbon fragment of IV may be modified in several ways to give different end-products. For example, oxidation at carbon atom (1) leads to the formation of cyanidin, at (3) to the flavone luteolin and at both (2) and (3), or at (1) and (3), to the flavonol quercetin.

Such a conception, implying a parallel rather than a sequential relationship between anthocyanins and anthoxanthins, has been shown to offer a more satisfactory explanation of the probable course of pigment production in *Dahlia* (Lawrence and Scott-Moncrieff 1935) than the earlier suggestions depending on the reduction of anthoxanthin to anthocyanin. It was possible to deduce from the results of this investigation that the *Dahlia* pigments of flavane type are synthesized from two components, one always present in adequate amount and another present in limited amount. This latter may be identified with the $C_6 . C_3$ intermediate which is the source of the unfused benzene nucleus; the former may be the source of the phloroglucinol nucleus. It should be emphasized that the hypothesis will be valid even if the end-products are not directly synthesized from simple carbohydrates. If they are derived from polysaccharides or other complexes, the states of oxidation should be equivalent in the absence of oxidation or reduction processes.



(I)



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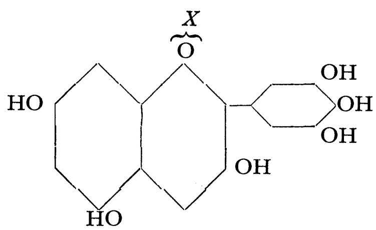
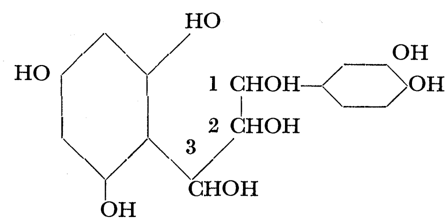


(III)



(IV)

The study of genetics in relation to flower colour appears at present to be one of the most fruitful lines along which the mechanism of synthesis of anthocyanins in the plant may be approached. If we could secure a convincing demonstration that cyanidin is the normal anthocyanidin type, with the corollary that the production *in vivo* of pelargonidin or of delphinidin involves at least one more stage than that of cyanidin, it would be of the utmost value in interpreting the genetical data.

Mixtures of anthocyanins based on one or more anthocyanidins

(1) In the majority of species which have been examined, pigmentation in any given part of a plant is due to one anthocyanin only. There are, however, a certain number of exceptions, in which a second constituent is present—usually in small proportion.

The simplest of such mixtures are of methylated mixed with partially methylated or unmethylated anthocyanins all derived from the same parent anthocyanidin; for example, malvin together with some petunin and delphin, or peonin containing traces of cyanin (cf. Table I). Where mixtures of malvidin (3′ : 5′-dimethoxydelphinidin), petunidin and delphinidin glycosides are encountered, and particularly when the proportions of the components may vary—as in *Lathyrus odoratus*—the malvidin and petunidin are evidently formed by a straightforward process of methylation, not necessarily of delphinidin itself, but perhaps of some intermediate, which in the absence of methylating agents would give rise to delphinidin. In other words, the essential steps in the syntheses of these three substances are the same, the difference lying in the fact that the complete syntheses of petunidin and malvidin require one stage more than that of delphinidin, namely, the methylating process.

It has been pointed out (Scott-Moncrieff 1936) that the presence or absence of certain structural characteristics of the anthocyanin molecule, and certainly the sugar types, is dependent upon the presence or absence of specific genes. Although there is no proof as yet that the presence or absence of *O*-methyl groups is controlled in this way, such an assumption is by analogy perfectly logical. If the reactions resulting in the methylation of one or more hydroxyl groups are determined by specific factors, then in the cases cited these genes cannot exert sufficient influence to enable the reactions to be carried to completion. This appears self-evident, but it has been emphasized in order to provide a parallel for cases of mixtures derived from different anthocyanidins, since it is known that the transition from one anthocyanidin to another, e.g. from pelargonidin to cyanidin, is genetically controlled. Hybrid and polyploid types such as *Dahlia* are possibly exceptional.

(2) Tables IIA and IIB give lists of plants in which the main cyanic constituent, based on either pelargonidin or delphinidin, contains varying amounts of cyanidin. Table III embraces mixtures in which definite identification of the minor constituent was impracticable, but it is clear that they all belong to the classes represented by Tables I and II. In these mixtures the presence of a second component in small amount may plausibly be regarded as due to the non-completion of one or more stages in the chain of reactions involved in the synthesis.* At first sight it may seem curious to regard the by-product as more simply constructed than the main product, but this hypothesis is, from a statistical point of view, the one that fits in best with the genetic data. If it is valid, the nature of the second component should throw some light on the relations between the synthesis *in vivo* of the three parent anthocyanidins; but before any conclusions can be drawn, two assumptions must be made:

(*a*) That the mode of synthesis of each anthocyanidin in any particular organ† is the same for different plants.

(*b*) That the syntheses of pelargonidin, cyanidin and delphinidin derivatives are

* This may not necessarily apply when two constituents are present in comparable proportions, as in *Lychnis*, *Papaver* and *Cestrum* spp., and these have not been included in the tables.

† For this reason only flowers are considered, though there are a few cases of mixtures in leaves and fruits.

along parallel lines, differing only in the processes determining the presence or absence of 3′- and 5′-hydroxyl groups.

The second of these assumptions is quite justifiable, the occurrence of "sports", for example, containing an anthocyanin based on an anthocyanidin other than the normal, is sufficient to show the close relationship. The first assumption is required by the existence of any correlation at all.

There are four possibilities concerning the number of steps required for the synthesis of pelargonidin, cyanidin and delphinidin derivatives, namely:

(A) Pelargonidin $<$ cyanidin $<$ delphinidin,
(B) Pelargonidin $>$ cyanidin $>$ delphinidin,
(C) Pelargonidin $>$ cyanidin $<$ delphinidin,
(D) Pelargonidin $<$ cyanidin $>$ delphinidin.

Of these four, (D) only conforms with assumption (*b*) in such an improbable manner that it may be disregarded.

Table I.* Mixtures of anthocyanins due to incomplete methylation

Althaea rosea vars.	Malv. Pet. and Delph. 3-mono-gluc. and di-gluc.
Lathyrus grandiflorus / *L. odoratus* vars.	Malv. Pet. and Delph. di-gluc.
Ceratostigma plumbaginoides	Malv. di-gluc. and some Pet. or Delph.
Geranium psilostemon	Malv. di-gluc. and trace Pet.
Iris Kaempferi var.	Malv. di-gluc. and trace Pet.
Limonium Suworowi	Malv. di-gluc. and trace Pet. or Delph.
Ixia speciosa var.	Pet. di-gluc. and trace Malv. or Delph.
Phlox Drummondii var.	Pet. 3-mono-gluc. and Malv. and Delph.
Pisum sativum vars.	Pet. di-gluc. and some Delph.
	Pet. di-gluc. and some Malv.
Lathyrus odoratus var.	Peon. di-gluc. and varying small amounts Cyan.
Anchusa azurea var. "Dropmore"	Delph. di-gluc. and trace meth.
Convolvulus minor	Delph. di-gluc. and trace meth.
Phlox Drummondii var.	Delph. di-gluc. and trace Pet. or Malv.

* Malv. = malvidin; Pet. = petunidin; Delph. = delphinidin; Peon. = peonidin; gluc. = glucoside; Cyan. = cyanidin; pent. gluc. = pentoseglucoside or methylpentoseglucoside or rhamnoside; Pel. = pelargonidin; Fe^{+} = anthocyanidin exhibiting a ferric reaction; bio. = bioside; mono- = monoglycoside, etc.; meth. = methylated derivative.

In Table II A the mixtures consist of delphinidin and cyanidin glycosides, and it will be seen that cyanidin derivatives occur as the minor components. On the above hypothesis this indicates that the synthesis of delphinidin requires at least one more stage than that of cyanidin. The plants in Table II B contain pelargonidin and cyanidin glycosides again with cyanidin derivatives as the minor constituents, indicating that the production of cyanidin also involves at least one stage less than that of pelargonidin. Hence (C) is the correct scheme. In Table II C are a few plants in which the anthocyanin is based on cyanidin, and is mixed with small proportions of derivatives of delphinidin or pelargonidin. Even so, in view of the small numbers the statistical argument holds. Taking these separately, the first four suggest that delphinidin is synthetically simpler than cyanidin, and the last one that pelargonidin is synthetically simpler than cyanidin. These conclusions are contradictory to one another as well as to scheme (C), so either the first assumption (*a*) is wrong, or all

Table II a. Mixtures of anthocyanins based on delphinidin and cyanidin

Aethionema grandiflora	Delph. di-gluc. and trace Cyan.
Billbergia Sanderiana	Delph. di-gluc. and trace Cyan.
Campanula Portenschlagiana	Delph. di-gluc. and trace Cyan.
Dictamnus albus var. *caucasicus*	Delph. 3-pent-gluc. and trace Cyan.
Echinops bannaticus	Delph. di-gluc. and trace Cyan.
Hyacinthus orientalis var. "King of the Blues"	Delph. di-gluc. and trace Cyan.
Pycnostachys Dawei	Delph. di-gluc. and trace Cyan.
Tropaeolum majus vars.	Delph. di-gluc. and Cyan. (varying proportions)
Verbena erinoides, *V. radicans*, *V. venosa*	Delph. di-gluc. and trace Cyan.
Streptocarpus Rexii	Malv. di-gluc. and trace Cyan.

Table II b. Mixtures of anthocyanins based on pelargonidin and cyanidin

Anthurium scherzerianum	Pel. 3-pent-gluc. and trace Cyan.
Clianthus Dampieri	Pel. 3-mono-gluc. and a little Cyan.
Hyacinthus orientalis var. "Queen of the Pinks"	Pel. di-gluc. and trace Cyan.

Table II c

Anemone coronaria var.	Cyan. di-gluc. and some Delph.
Callistemon speciosus	Cyan. di-gluc. and some Delph.
Brunfelsia grandiflora	Cyan. di-gluc. and some Malv.
Iberis umbellata	Cyan. di-gluc. and a little Malv.
Chaenomeles japonica var.	Cyan. 3-pent-gluc. and a little Pel.

Table III. Mixtures of anthocyanins in which the second constituent was not identified

Boronia elatior	Malv. di-gluc. and a trace Fe^{+} anthocy.
Lythrum Salicaria	Malv. di-gluc. and a trace Fe^{+} anthocy.
Salvia pratensis	Malv. di-gluc. and a trace Fe^{+} anthocy.
Sempervivum arachnoideum	Malv. 3-pent-gluc. and some Fe^{+} anthocy.
Vriesia Duvaliana (bracts)	Malv. di-gluc. and some Fe^{+} anthocy.
Rhododendron Augustini, *R. californicum*, *R. oreotrephes*	Malv. di-gluc. and some Pet. or Cyan.
Callistephus hortensis var.	Delph. di-gluc. and a trace Cyan. or methylated anthocy.

the possibilities have not been taken into account. At the bottom of Table I are three plants whose flowers contain delphinidin diglycoside together with *small* amounts of methylated derivatives. Here the non-completion of the methylating process is evidently carried to a point where it is almost entirely inhibited. Such an idea, the occasional existence of an inhibiting factor, is quite in keeping with the experience of plant geneticists. For example, in flowers of *Primula sinensis*, colour due to anthocyanins may be partially or almost completely suppressed by the action of an inhibiting factor. If the plants in Table IIc are regarded as analogues of *Anchusa azurea*, etc., then not only are the results reconcilable with one another, but at the same time they cease to contradict the inference that scheme (C) is correct. It might be objected that all the mixtures are similarly due to inhibition, but if this is so we are faced with contradictory conclusions from Tables IIa and IIb and with the *reductio ad absurdum* that certain of the mixtures in Table I are due to inhibited demethylation rather than incomplete methylation.* Hence the only way in which the great majority of the above results can be correlated is on a basis which leads to the conclusion that cyanidin is the anthocyanidin whose synthesis requires the least number of steps. In the light of this, it is significant that there is not a single case, which could be legitimately included, where mixtures of anthocyanins based on pelargonidin and delphinidin have been found, and this fact gives strong support to our arguments.

Only species and varieties of species have been included in the lists given in this paper. Anything which is known to arise from species hybridization, or whose origin is in doubt, has been omitted, since it is known that hybridization may give rise to anomalous results. There are two cases in which malvidin-pelargonidin mixtures have been found, namely, forms of *Pelargonium zonale* and *Primula sinensis*. The zonal pelargoniums Henry Jacoby and Madame de Monier are known to be hybrids, and all *Pelargonium* spp. examined contain either pure malvidin or pelargonidin glycosides. *Primula sinensis*, on the other hand, has never been artificially hybridized with any other species, and many of its varieties contain pure anthocyanins. However, a recent mutant known as Dazzler gives rise to mixtures of pelargonidin and malvidin 3-monosides in certain of its progeny (Scott-Moncrieff 1936). This is easily explained, as breeding results show that the Dazzler mutation produces pelargonidin quite independently of, and superimposed upon, the normal pigmentation which may be either pelargonidin or malvidin. Hence the two cases where mixtures of anthocyanins based on pelargonidin and delphinidin occur do not come within the sphere of discussion. It is possible that cases where mixtures of anthocyanins derived from two anthocyanidins occur in comparable proportions, such as *Papaver*, *Cestrum* and *Lychnis* spp.,

* Another cause of apparently anomalous results is the heterogeneous distribution of the anthocyanins in the flowers; in many cases the whole of the flower petals was taken for the analysis. Dark spots (and sometimes anthers, or corolla tube) may contain anthocyanins differing from those in the rest of the petals. Again, local stabilizing factors may be operative. Examples in *Lathyrus odoratus* are relevant to degree of methylation. Co-pigment tends to concentrate in the wings of the flowers and cases have been encountered in which the proportion of malvin to petunin is greater in the wings than in the standards of the same flowers. We suggest that malvin forms a more stable compound with the flavonol derivative than does petunin and that where flavonols are present the malvin, relatively to petunin, is protected from destruction. This is confirmed experimentally by the observed greater effect of co-pigments on malvin as compared with petunin.

are analogous to the Dazzler forms of *Primula sinensis*. This is in fact known to be so in *Papaver Rhoeas* (Scott-Moncrieff 1936).

Therefore, subject to certain assumptions, the only conclusion which can be drawn from the evidence of mixed anthocyanidin derivatives is that cyanidin is the anthocyanidin whose synthesis in the plant involves at least one stage less than that of either pelargonidin or delphinidin (scheme C).

Leuco-anthocyanins

Since the colours of flowers and fruits, in attracting insects and birds, play an important part in the reproduction of the species, it is clear that natural selection, following upon variation, will operate to perpetuate and increase the number of colour types adaptable to reproductive needs. Selection for colour obviously cannot take place directly with leuco-anthocyanins though it may do so indirectly if these substances are precursors of the flower and fruit pigments. The presence in seeds of some varieties of *Lathyrus odoratus* of leuco-anthocyanins, derived from the same anthocyanidins as are the anthocyanins in the flowers, may indicate a biological relation between the leuco- and normal anthocyanins. But this need not imply that the one is a precursor of the other, and the following points indicate that it is not:

(1) The leuco-anthocyanins are morphologically much more widespread than the normal anthocyanins; for example, they occur in wood, bark and nutshells as well as in flowers, leaves and fruits.

(2) In certain cases where both normal and leuco-anthocyanins are present in the same part of a plant, the normal anthocyanin is not derived from the same anthocyanidin as the leuco-anthocyanin.

(3) Certain leuco-anthocyanin types, for example, peltogynol (Robinson and Robinson 1935), have no counterpart in the anthocyanins.

In this latter respect they resemble the flavones and flavonols, and it is perhaps worth while to draw attention once again to the fact that quercetin (3′ : 4′-dihydroxybenzene nucleus) is the most frequently encountered anthoxanthin.* The anthocyanidins obtained from leuco-anthocyanins in the species examined (Robinson and Robinson 1933, 1934) were as follows:

Pelargonidin	in	2 spp.
Cyanidin	in	42 spp.
Petunidin	in	1 sp.
Delphinidin	in	5 spp.

Thus the cyanidin orientation occurs with a frequency of 84%. In addition, peltogynol, with a catechol nucleus, was found in four species, and from some others an anthocyanidin tallying with 6-hydroxycyanidin was formed. In the two cases in which

* Gisvold and Rogers (1938) give figures showing that in 268 cases where anthoxanthins have been identified, 220 had the 3′ : 4′-dihydroxy orientation in the substituted phenyl group.

both normal and leuco-anthocyanins were examined in the same part of a plant, namely, the flowers of a variety of *Hydrangea opuloides* and the fruits of *Vitis heterophylla*, the former contained a delphinidin glycoside* and the latter malvidin 3 : 5-dimonoside, but the leuco-anthocyanins from both yielded cyanidin. While a leuco-anthocyanin → pelargonidin was found in the seeds of a variety of *Lathyrus odoratus* whose flowers contained a glycoside of pelargonidin, and a leuco-anthocyanin → petunidin in the seeds of a variety whose flowers contained a glycoside of petunidin, the seeds of a white-flowered variety contained a leuco-anthocyanin → cyanidin, although there are no *L. odoratus* varieties with flowers pigmented by cyanidin glycosides as main constituent.

Further, there are a few cases where mixtures were obtained from leuco-anthocyanins, analogous to those found with normal anthocyanins:

Dipterocarpus zeylanicus (bark): Delph. and some Cyan.
Eucalyptus tereticornis (wood): Delph. and some Cyan. or methylation.
Entandrophragema macrophyllum (wood): Delph. and some methylation or Cyan.
Pterocarpus marsupium (kino): Cyan. and a little Delph.
Syncarpia laurifolia (wood): Cyan. and some Delph.

Since it is improbable that selection has much influence on the frequency of occurrence of the respective types, the above data afford good evidence that the cyanidin structure is the one most readily produced in the plant.

Leaves and fruits

It is clear that selection must play an important part in determining the relative frequency with which pelargonidin, cyanidin and delphinidin types occur in flowers and fruits. Here the possibility of advantage is apparent and is bound up with reproduction. In leaves, however, it is questionable whether anthocyanin serves any useful function, and even if it does, we do not know that any particular degree of oxidation would be more advantageous than another. In the absence of information on this point, it is necessary to differentiate between

(A) permanently pigmented leaves,
(B) autumnal coloration, and
(C) young leaves which contain anthocyanins, but become green on maturing.

(B) and (C) are transient, and it is probable that the presence of anthocyanin is incidental upon an increased carbohydrate concentration. (A), however, may be of some little value; if only on account of its permanence it is possibly more important than (B) and (C).

On this basis, it is interesting to note the frequency with which cyanidin occurs in the various types of leaves as compared with flowers and fruits. The figures represent

* After exhaustive purification this anthocyanin is revealed as delphinidin 3-monoside.

the number of genera in which cyanidin has been found expressed as a percentage of the total number of genera examined:

Autumn leaves	95
Young leaves	93
Permanently pigmented leaves	80
Fruits	69
Flowers	50

It has already been stated that the anthocyanins in fruits and flowers are of definite value to the plant, and that there is little or no reason for supposing that they are of

TABLE IV. ANTHOCYANINS PRESENT IN PERMANENTLY PIGMENTED LEAVES*

76–264	*Coleus Blumei* Benth. vars.	Cyan. di-glyc. A.
	Perilla nankinensis Decne	Cyan. 3 : 5-di-A.
	P. ocimoides Linn. var. *crispa* (Kuroda and Wada 1936)	Cyan. 3 : 5-di-A.
75–259	*Aphelandra nitens* Hook. f.	Delph. di-
	Strobilanthus Dyerianus Hort.	Cyan. 3 : 5-di-
256	*Columnea Schiedeana* Schlecht.	Cyan. di-
	Streptocarpus Wendlandii Spreng.	Cyan. 3-bio.
252	*Antirrhinum majus* Linn. vars.	Cyan. 3-pent.gluc. Pel. 3-pent.gluc.
69–240	*Primula sinensis* Lindl. vars.	Malv. 3-bio- Pel. 3-bio.
67–238	*Hieracium Lima* Haub.	Cyan. 3-mono-
66–233	*Viburnum tomentosum* Thunb. var. *plicatum*	Cyan. 3-mono-
232	*Hoffmannia Ghiesbreghtii* Hemsl. var. *variegata*	Cyan. 3-pent.gluc.
65–231	*Hoya carnosa* R.Br. var. *variegata*	Cyan. 3-pent.gluc.
59–213	*Chaerophyllum anthriscus* Lam.	Cyan. 3 : 5-di-
54–193	*Cissus discolor* Blume.	Malv. di-
48–163	*Fagus sylvatica* Linn. var.	Cyan. 3-mono-
40–143	*Prunus persica* Stokes var.	Cyan. 3-mono-
	P. divaricata Ledeb. var. *Pissardii*	Cyan. 3-mono-
39–132	*Hydrangea opuloides* Koch. vars.	Cyan. 3-bio.
38–136	*Acalypha macrostachya* Jacq.	Cyan. 3-mono-
36–132	*Hibiscus rosa-sinensis* Linn. var. *Cooperii*	Cyan. 3-mono-A.
33–120	*Centradenia grandiflora* Endl.	Malv. 3 : 5-di-A.
30–104	*Begonia coccinea* Hook.	Cyan. 3-bio.
21– 77	*Fuchsia triphylla* Linn.	Malv. 3 : 5-di-
20– 67	*Geranium robertianum* Linn.	Cyan. 3-bio.
11– 39	*Crambe maritima* Linn.	Cyan. 3 : 5-di-
96–313	*Cordyline terminalis* Kunth.	Cyan. 3 : 5-di-A.
	C. terminalis var.	Malv. di-A.
91–102	*Alocasia Lowii* Hook.	Cyan. 3-bio.
	Anthurium Scherzerianum Schott	Pel. 3-pent.gluc.
88–292	*Calathea insignis* Bull.	Delph. 3-pent.gluc.
	Stromanthe Porteana A. Gris. var. *variegata*	Cyan. 3-pent.gluc.
291	*Canna indica* Linn.	Cyan. 3-pent.gluc.
84–280	*Cyanotis kewensis* C. B. Clarke	Cyan. 3-bio.
	Rhoeo discolor Hance	Cyan. 3-bio.
	Zebrina pendula Schnitzl.	Cyan. 3-bio.

* Numbers are those given by Hutchinson for orders and families. A. = acylated.

any importance as such in young and autumn leaves, therefore the above figures strongly support our contention that cyanidin is the simplest of the three anthocyanidin types.

The data on young leaves (Price and Sturgess 1938) and autumn leaves (Lawrence *et al.* 1938) have already been published in collected form; those for permanently pigmented leaves, fruits and flowers, are shown in Tables IV, V and VI respectively.

Flowers

The majority of the plants whose flowers have been examined are those commonly grown in gardens. They have therefore been subjected to selection towards the extremes of colour, thus favouring an excess of pelargonidin and delphinidin types at the expense of cyanidin. In spite of this the figures clearly illustrate the predominance of cyanidin. The frequency of occurrence of the three types, expressed in terms of percentages of the total numbers of orders, families, genera and species examined, is shown in Table VII and fig. 1. The effect of artificial selection is demonstrated by the fact that while over 50 % of the species examined contain delphinidin derivatives, yet as the scope of the subdivisions is increased to genera, families and orders cyanidin proves to be the more widespread.

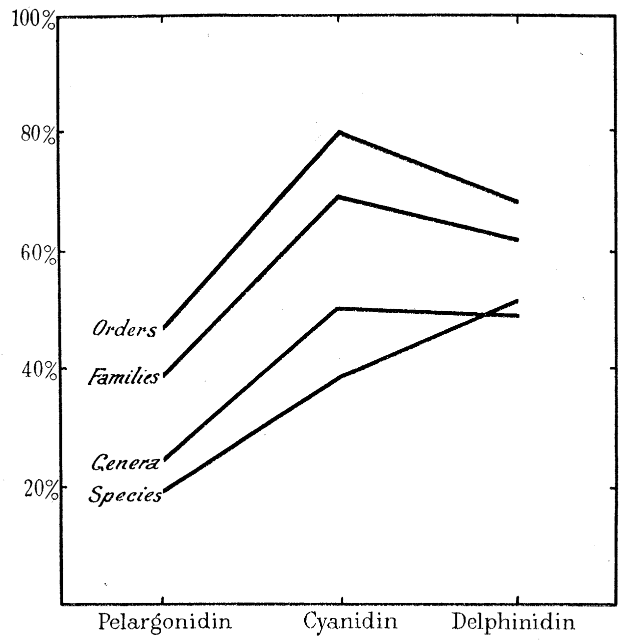


Fig. 1

The complete list of flowers examined (Table VI) is based on the system of classification put forward by Hutchinson (Hutchinson 1926). The dicotyledons are arranged in two major divisions, the Archichlamydeae and the Metachlamydeae. The plants in the latter are, on the whole, the more highly developed and widely variable. One

Table V. Anthocyanins present in fruits

74–250	*Solanum melongena* Linn.	Delph. 3-pent.gluc.
	var. *erculentum* (Kuroda and Wada 1936)	Delph. 3-bio.
66–233	*Leycesteria formosa* Wall.	Cyan. 3 : 5-di-
	Lonicera nitida E. H. Wils.	Cyan. 3-bio.
	Sambucus nigra Linn. (Nolan and Casey 1931)	Cyan. 3-pent.gluc. and mono-
	S. racemosa Linn.	Cyan. 3 : 5-di-
	Viburnum Tinus	Cyan. 3-mono-
64–229	*Ligustrum vulgare* Linn.	Delph. ? sugar
62–223	*Ardisia crispa* A.DC.	Cyan. 3-mono-
60–216	*Oxycoccus macrocarpus* Pers. (Grove and Robinson 1931)	Peon. 3-mono-
	Vaccinium Myrtillus Linn. (Karrer and Widmer 1927*a*)	Malv. 3-mono-
	V. Vitis-Idaea Linn. (Willstätter and Mallison 1915*a*)	Cyan. 3-mono-
59–212	*Hedera helix* Linn.	Cyan. 3-bio.
59–209	*Cornus mas* Linn.	Pel. 3-mono-
54–193	* *Vitis hederacea* Ehrh.	Cyan. ? sugar A.
	* *V. quinquefolia* Lam. (Willstätter and Zollinger 1916*b*)	Malv. 3-mono-
	V. vinifera Linn. (Willstätter and Zollinger 1915, 1916*b*)	Malv. 3-mono-
	V. labrusca Linn. (Shriner and Anderson 1928)	Malv. 3-mono-
	V. riparia Michx. (Shriner and Anderson 1928)	Malv. 3-mono-
	V. aestivalis Michx. (Shriner and Anderson 1928)	Malv. 3-mono-
	V. heterophylla Thunb.	Malv. 3 : 5-di-
51–173	*Euonymus japonicus* Thunb. (aril)	Cyan. ? sugar
	E. yedoensis Koehne (capsule)	Cyan. 3-mono-
171	*Ilex aquifolium* Linn.	Pel. 3-bio.
50–167	*Ficus carica* Linn.	Cyan. 3-mono-
	Morus nigra Linn.	Cyan. 3-mono-
41–148	*Pisum sativum* Linn. vars. (pods)	Cyan. 3 : 5-di- Delph. di-
40–143	*Cotoneaster frigida* Wall.	Cyan. 3-pent.gluc.
	C. Simonsii Baker.	Pel. 3-pent.gluc.
	Crataegus intricata Lange	Cyan. 3-mono-
	C. macracantha Lodd.	Cyan. 3-mono-
	C. orientalis Pall.	Cyan. 3-mono-
	C. oxyacantha Linn. var. *rosea plena*	Cyan. 3-mono-
	Fragaria vesca Linn.	Pel. 3-mono-
	F. virginiana Duch.	Pel. 3-mono-
	Prunus avium Linn. var.	Cyan. 3-mono-
	P. communis Fritsh. var.	Cyan. 3-mono-
	P. spinosa Linn. (Willstätter and Zollinger 1916*a*)	Cyan. 3-pent.gluc.
	Pyracantha coccinea Roem. var. *Lalandi*	Cyan. 3-pent.gluc.
	Rubus idaeus Linn. vars.	Cyan. 3-bio.
21–75	*Punica granatum* Linn.	Delph. di-
5–19	*Berberis aquifolium* Pursh.	Delph. 3-mono-
	B. Darwinii Hook.	Pet. 3-mono-
	B. vulgaris Linn.	Pel. 3-mono-
88–287	*Musa coccinea* Andr.	Pel. 3-mono-

* These names are synonymous, but we have used them because of the uncertainty as to the origin of the material.

TABLE VI. LIST OF ANTHOCYANINS PRESENT IN FLOWERS OF SPECIES AND VARIETIES OF MONOCOTYLEDONS AND DICOTYLEDONS

DICOTYLEDONS	Pelargonidin	Cyanidin	Malvidin	Delphinidin	Comments
LAMIALES					
LABIATEAE					
Ajuga reptans Linn.	—	—	—	di-A.	—
Brunella grandiflora Jacq. vars.	—	di-A.	—	di-	—
Coleus shirensis Gürke	—	—	—	di-A.	—
Lamium maculatum Linn. (Schmidt and Körperth 1936)	3-pent.gluc.	—	—	—	—
L. purpureum Linn.	—	3 : 5-di-	—	—	—
Lavandula spica Cav. var. *nana*	—	—	—	di-	—
L. vera DC.	—	—	—	di-	—
Monarda didyma Linn. (Karrer and Widmer 1927*b*) and var. "Cambridge Scarlet"	3 : 5-di-A.	—	—	—	—
Nepeta Mussinii Spreng.	—	—	—	di-A.	—
N. ucranica Linn.	—	—	—	di-A.	—
Origanum vulgare Linn.	—	—	di-	—	—
Pycnostachys Dawei N.E.Br.	—	—	—	di-A.	—
Rosmarinus officinalis Linn.	—	—	—	di-A.	—
Salvia coccinea Juss. (Willstätter and Bolton 1916*a*)	3 : 5-di-A.	—	—	—	—
S. Grahamii Benth.	3 : 5-di-A.	—	—	—	—
S. nemorosa Crantz	—	—	di-A.	—	—
S. neurepia Fernald.	3 : 5-di-A.	—	—	—	—
S. patens Cav. (Reynolds *et al.* 1934)	—	—	—	di-	—
S. pratensis Linn.	—	—	3 : 5-di	—	—
S. splendens Ker-Gawl (Willstätter and Bolton 1916*a*)	3 : 5-di-A.	—	—	—	—
Scutellaria violacea Heyne	—	—	—	di-A.	—
Stachys sylvatica Linn.	—	3-mono-	—	—	—
Thymus serpyllum Linn. var. *coccineus*	—	3 : 5-di-	—	—	—
VERBENACEAE					
Clerodendron fallax Lindl.	3-bio.	—	—	—	—
Lippia nodiflora Michx.	—	—	—	di-	—
Verbena canadensis Brit.	—	3 : 5-di-	—	—	—
var. *Drummondii*	—	3 : 5-di-	—	—	—
V. chamaedrifolia Juss.	3-mono-	—	—	—	—
V. erinoides Lam.	—	—	—	di-	—
V. radicans Gill. and Hook.	—	—	—	di-	—
V. tenera Spreng.	—	3 : 5-di-	—	—	—
V. venosa Gill. and Hook.	—	—	—	di-	—
PERSONALES					
ACANTHACEAE					
Aphelandra nitens Hook.	3-mono-	—	—	—	—
Beloperone guttata T. S. Brandegee	—	3-pent.gluc.	—	—	—
Hypoëstes aristata R.Br.	—	3 : 5-di-	—	—	—
Peristrophe speciosa Nees.	—	3 : 5-di-	—	—	—
Thyrsacanthus rutilans Planch.	3-pent.gluc.	—	—	—	—
BIGNONIACEAE					
Bignonia speciosa Grah.	—	A? sugar	—	—	—
Jacaranda ovalifolia R.Br.	—	—	—	di-	—
Spathodea nilotica Seem.	3-mono-	—	—	—	—

TABLE VI (*cont.*)

DICOTYLEDONS	Pelargonidin	Cyanidin	Malvidin	Delphinidin	Comments
PERSONALES (*cont.*)					
GESNERIACEAE					
Gesneria cardinalis Lehm.	*	—	—	—	*Gesnerin
Isoloma hirsutum Regel.	3-pent.gluc.	—	—	—	—
Naegelia cinnabarina Lindl.	3-mono-	—	—	—	—
N. zebrina Regel var. *discolor*	3-pent.gluc.	—	—	—	—
Ramonda pyrenaica Rich. ex Pers.	—	—	—	di-	—
Sinningia speciosa Hiern. vars.	3-bio.*	3-pent.gluc.	3-bio.*	—	*Also 3-pent. gluc.
Streptocarpus caulescens Vatke	—	—	3 : 5-di-	—	—
S. Dunnii Mast.	—	3-pent.gluc.	—	—	—
S. Rexii Lindl.	—	—	3 : 5-di-	—	—
S. Wendlandii Spreng.	—	—	3 : 5-di	—	—
SCROPHULARIACEAE					
Antirrhinum majus Linn. vars. (Scott-Moncrieff 1930)	—	3-pent.gluc.	—	—	—
Digitalis purpurea Linn.	—	3 : 5-di-	—	—	—
Erinus alpinus Linn.	—	—	—	di-	—
Linaria purpurea Mill	—	—	—	di-	—
Mimulus cardinalis Dougl.	3-mono-	—	—	—	—
Nemesia strumosa Benth. scarlet var.	—	3-mono-	—	—	—
Penstemon Barrettae Hort.	—	—	—	di-	—
P. cordifolius Benth.	—	3 : 5-di-	—	—	—
P. heterophyllus Lindl.	—	—	—	di-	—
P. isophyllus Robinson	3 : 5-di-	—	—	—	—
P. platyphyllus Rydb.	—	—	—	di-	—
Rehmannia angulata Hemsl.	—	3-pent.gluc.	—	—	—
Rhodochiton volubile Zucc.	—	3-mono-	—	—	—
Scrophularia nodosa Linn.	—	3-bio.	—	—	—
Torenia Fournieri Lindl. var. *grandiflora*	—	3 : 5-di-	—	—	—
Verbascum phoeniceum Linn.	—	*	—	—	*Peon.-3-mono-
Veronica chamaedrys Linn.	—	—	—	di-	—
V. maritima Linn.	—	—	—	di-	—
V. teucrium Linn. var. *rupestris*	—	—	—	di-	—
SOLANALES					
CONVOLVULACEAE					
Convolvulus sepium Linn.	—	3-mono-	—	—	—
C. tricolor Linn.	—	—	—	di-	—
Ipomoea Horsfalliae Hook. var. *Briggsii*	3 : 5-di-	—	—	—	—
I. Learii Paxt.	—	—	3 : 5-di-	—	—
I. tricolor Cav.	—	—	di-	—	—
Pharbitis nil Choisy. vars. (Kataoko 1927–8)	? sugar	*	—	—	*Peon. ? sugar
SOLANACEAE					
Browallia demissa Linn.	—	—	—	di-A.	—
B. elata Linn.	—	—	—	3 : 5-di-A.	—
Brunfelsia calycina Benth. var. *macrantha*	—	—	3 : 5-di-	—	—
B. grandiflora D. Don.	—	di-	—	—	—
Nierembergia coerulea Gill.	—	—	—	di-	—
N. frutescens Dur.	—	—	—	di-	—
*Salpiglossis sinuata** Ruiz and Pav. and vars.	—	—	—	di-	*Pet. di-A. or Pet. di-
Solanum crispum Ruiz and Pav.	—	—	—	di-*	—
S. dulcamara Bentl. and Trimen.	—	—	—	di-	—

TABLE VI (*cont.*)

DICOTYLEDONS	Pelargonidin	Cyanidin	Malvidin	Delphinidin	Comments
BORAGINALES					
BORAGINACEAE					
Anchusa italica Retz. var. "Dropmore"	—	—	—	di-	—
Lithospermum prostratum Loisel.	—	—	—	*	*Pet. di-
Myosotis sylvatica Hoffm. var. "Blue King"	—	—	—	di-	—
Pulmonaria angustifolia Linn. var. *azurea*	—	—	—	di-	—
Symphytum caucasicum Bieb.	—	—	—	di-	—
S. officinale Linn. (Schmidt and Körperth 1936)	di-	—	—	—	—
POLEMONIALES					
HYDROPHYLLACEAE					
Nemophila insignis Benth.	—	—	—	di-	—
Phacelia Whitlavia A. Gray	—	—	3 : 5-di-	—	—
POLEMONIACEAE					
Gilia capitata Douglas	—	—	—	di-	—
Phlox divaricata Linn. var. *Laphami*	—	—	—	3 : 5-di-	—
P. Drummondii Hook. vars.	—	—	—	di-*	*And Pet.-3-mono-
CAMPANALES					
CAMPANULACEAE					
Campanula glomerata Linn.	—	—	—	di-	—
C. medium Linn. pink var.	3-bio.	—	—	—	—
C. persicifolia Linn. var. "Telham Beauty"	—	—	—	di-	—
C. Portenschlagiana Roem. & Schult.	—	—	—	di-	—
C. pusilla Haenke	—	—	—	di-	—
Platycodon grandiflorum DC. var. "Mariesii"	—	—	—	di-	—
LOBELIACEAE					
Lobelia cardinalis Linn. vars.	3-mono-	—	—	—	—
L. erinus Linn. var. "Crystal Palace"	—	—	—	di-	—
PRIMULALES					
PLUMBAGINACEAE					
Ceratostigma plumbaginoides Bunge	—	—	di-	—	—
Limonium sinuatum Mill and var. *roseum**	—	—	—	di-	*var. 3-pent. gluc.
L. Suworowi O. Ktze.	—	—	3-mono-	—	—
Plumbago rosea Linn.	—	*	—	—	*Peon.-3-mono-A.
P. capensis Thunb.	—	3 : 5-di-	—	—	—
Statice armeria Linn.	—	—	di-	—	—
PRIMULACEAE					
Anagallis arvensis Linn. and blue var.*	3-mono-	—	3-mono-*	—	—
A. coerulea Schreb.	—	—	3 : 5-di-	—	—
A. collina Ball	3-mono-	—	—	—	—
Cyclamen persicum Mill. (Karrer and Widmer 1927 *a*) and vars.*	—	*	3- (and 3 : 5-)	—	*Peon. 3-pent. gluc.
Dodecatheon integrifolium Michx.	—	—	di-	—	—

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

TABLE VI (*cont.*)

DICOTYLEDONS	Pelargonidin	Cyanidin	Malvidin	Delphinidin	Comments
PRIMULALES (*cont.*)					
PRIMULACEAE (*cont.*)					
Primula acaulis Hill. vars. (Scott-Moncrieff 1936)	—	—	3-mono-	—	—
P. burmanica I. B. Balf and Ward	—	—	3 : 5-di-	—	—
P. Cockburniana Hemsl.	—	3 : 5-di-	—	—	—
P. crispata I. B. Balf and W. W. Sm.	—	—	*	—	*Hirsutin
P. denticulata Smith	—	—	*	—	*Hirsutin
P. Forrestii Balf	—	—	3 : 5-di-	—	—
P. frondosa Janka.	—	—	*	—	*Hirsutin
P. hirsuta All. (Karrer and Widmer 1927*c*)	—	—	*	—	*Hirsutin
P. integrifolia Linn. (Karrer and Widmer 1927*c*)	—	—	3 : 5-di-	—	—
P. japonica Gray vars.	—	—	3 : 5-di-*	—	*And 3-pent. gluc.
P. malacoides Franch. vars.	—	—	3 : 5-di-	—	—
P. mollis Nutt.	—	—	3 : 5-di-	—	—
P. obconica Hance vars.	—	—	—	di-	—
P. rosea Royle	—	—	*	—	*Hirsutin
P. sinensis Lindl. vars. (Scott-Moncrieff 1936)	3-mono-	—	3-mono-	—	—
P. Veitchii Duthie	—	—	3 : 5-di-	—	—
P. viscosa All. (Karrer and Widmer 1927*c*)	—	—	3 : 5-di-	—	—
P. Waltonii Watt	—	—	3 : 5-di-	—	—
P. Wilsonii Dunn	—	—	3 : 5-di-	—	—
GENTIANALES					
GENTIANACEAE					
Gentiana acaulis Linn. (Karrer and Widmer 1927*b*)	—	—	—	3-mono-A.	—
G. campestris Linn.	—	—	—	3-pent.gluc.	—
G. septemfida Pall. var. *Lagodechiana*	—	—	—	di-	—
G. sino-ornata I. B. Balf	—	—	—	di-A.	—
ASTERALES					
COMPOSITAE					
Bellis perennis Linn. var. "Rob Roy"	—	3-bio.	—	—	—
Brachycome iberidifolia Benth.	—	—	—	di-	—
Callistephus hortensis Cass. vars. (Wit 1936)	3- and 3 : 5-	3- and 3 : 5-	—	3- and 3 : 5-	—
Carduus lanceolatus Linn.	—	3 : 5-di-	—	—	—
Centaurea cyanus Linn. (Willstätter and Everest 1913) and *Centaurea cyanus* pink var. (Willstätter and Mallison 1915*b*)*	3 5-di-*	3 : 5-di-	—	—	—
C. montana Linn.	—	3 : 5-di-	—	—	—
C. nigra Linn.	—	di-	—	—	—
Charieis heterophylla Cass.	—	—	—	di-	—
Chrysanthemum indicum Linn. (Willstätter and Bolton 1916*b*)	—	3-mono-	—	—	—
C. tricolor Andr.	—	3-mono-	—	—	—
Cichorium Intybus Linn.	—	—	—	di-	—
Dahlia coccinea Cav. (Lawrence and Scott-Moncrieff 1935)	3 : 5-di-	—	—	—	—

TABLE VI (*cont.*)

DICOTYLEDONS	Pelargonidin	Cyanidin	Malvidin	Delphinidin	Comments
ASTERALES (*cont.*)					
COMPOSITAE (*cont.*)					
D. coronata Hort. (Scott-Moncrieff 1936)	3-mono-	—	—	—	—
D. imperialis Roezl. (Lawrence and Scott-Moncrieff 1935)	—	3 : 5-di-	—	—	—
D. Merckii Lehm. (Lawrence and Scott-Moncrieff 1935)	—	3 : 5-di-	—	—	—
D. variabilis Desf.	3 : 5-di-	3 : 5-di-	—	—	—
Dimorphotheca aurantiaca DC.	—	—	—	3-mono-	—
Echinops bannaticus Rochel.	—	—	—	di-	—
Erigeron speciosus DC.	—	—	—	di-	—
Helichrysum bracteatum Andr.	—	3-mono-	—	—	—
Helipterum Manglesii Muell.	—	3 : 5-di-	—	—	—
Senecio speciosus Willd.	—	di-	—	—	—
DIPSACACEAE					
Scabiosa arvensis Linn.	—	—	—	di-	—
VALERIANACEAE					
Kentranthus ruber Lam. and DC.	—	? sugar	—	—	—
Valeriana officinalis Linn.	—	3-pent.gluc.	—	—	—
RUBIALES					
CAPRIFOLIACEAE					
Lonicera sempervirens Linn.	—	3 : 5-di-	—	—	—
RUBIACEAE					
Burchellia capensis R. Br.	—	3-pent.gluc.	—	—	—
Leycesteria formosa Wall. (calyx)	—	3 : 5-di-	—	—	—
Luculia gratissima Sweet	—	—	3 : 5-di-	—	—
Pentas coccinea Stapf.	—	3-bio.	—	—	—
LOGANIALES					
LOGANIACEAE					
Buddleia amplissima Hort.	—	—	—	di-	—
B. Colevilei Hook. and Thoms.	—	3-pent.gluc.	—	—	—
B. Davidii Franch. var. *magnifica*	—	—	—	di- and pet. 3-pent.gluc.	—
B. Davidii var. *superba*	—	—	—	*	*Pet.-di-
ERICALES					
EPACRIDACEAE					
Epacris longiflora Cav. var. *superba*	—	3-mono-	—	—	—
ERICACEAE					
Erica curviflora Salisb. var. *Burchellii*	—	3-pent.gluc.	—	—	—
E. gracilis Salisb.	—	3-mono-	—	—	—
E. hyemalis Hort.	—	3-mono-	—	—	—
Macleania punctata Hook.	3-mono-	—	—	—	—
Pentapterygium serpens Klotzsch	—	3-mono-	—	—	—
Rhododendron Augustinii Hemsl.	—	—	3 : 5-di-	—	—
R. californicum Hook.	—	—	3 : 5-di-	—	—
R. euchaites Balf. f. and Forrest	—	3-mono-	—	—	—
R. Griersonianum Balf. f. and Forrest	—	3-mono-	—	—	—
R. indicum Sweet. vars.	—	3- and 3 : 5-	—	—	—
R. oreotrephes W. W. Sm.	—	—	3 : 5-di-	—	—
R. rhodora S. F. Gmelin	—	—	—	3-mono-	—
R. Thomsonii Hook. f.	—	3-mono-	—	—	—
R. yunnanense Franch.	—	3-mono-	—	—	—

TABLE VI (*cont.*)

DICOTYLEDONS	Pelargonidin	Cyanidin	Malvidin	Delphinidin	Comments
SAPINDALES					
HIPPOCASTANACEAE					
Aesculus Hippocastanum Linn.	—	3-pent.gluc.	—	—	—
RUTALES					
RUTACEAE					
Boronia elatior Bartl.	—	—	3 : 5-di-	—	—
Correa speciosa Ait. var. *ventricosa*	—	3-pent.gluc.	—	—	—
Dictamnus albus Linn. var. *caucasicus*	—	—	—	3-pent.gluc.	—
RHAMNALES					
RHAMNACEAE					
Ceanothus Veitchianus Hook.	—	—	—	di-	—
LEGUMINOSAE					
Amherstia nobilis Wall.	3-pent.gluc.	—	—	—	—
Cercis siliquastrum Linn. (petals and sepals)	—	—	di-	—	—
Clianthus Dampieri A. Cunn.	3-mono-	—	—	—	—
Galega officinalis Linn.	—	—	—	di-	—
Lathyrus grandiflorus Sibth. and Sm.	—	—	di-*	—	*Containing pet. and delph.
L. latifolius Linn.	—	—	di-	—	—
L. odoratus Linn. vars.	3 : 5-di-	*	3 : 5-di-	—	*Peon.-3 : 5-di-
L. tingitanus Linn.	—	—	di-	—	—
L. undulatus Boiss.	—	—	3 : 5-di-	—	—
L. vernus Bernh. (Schmidt and Körperth 1936)	3-pent.gluc.	—	—	—	—
Lotus corniculatus Linn.	—	3-mono-	—	—	—
Ononis spinosa Linn.	—	—	3-pent.gluc.	—	—
Phaseolus multiflorus Willd. var. *vulgaris*	3-bio-	—	—	—	—
Pisum sativum Linn. vars.	—	—	—	*	*Pet. di-
Trifolium pratense Linn. var. "Early Red"	—	3-bio.	—	—	—
Vicia Cracca Linn.	—	—	—	di-	—
Wistaria chinensis DC.	—	—	—	di-	—
ROSALES					
ROSACEAE					
Chaenomeles japonica Lindl. vars.	3-pent.gluc.	3-pent.gluc.	—	—	—
Crataegus oxyacantha Linn. var. fl.pl. *rosea*	—	3-mono-	—	—	—
Malus sylvestris Mill. var. *aldenhamensis*	—	3-mono-	—	—	—
Potentilla atrosanguinea Wall.	—	3-mono-	—	—	—
P. nepalensis Hook.	—	3-mono-A.	—	—	—
P. nepalensis var. *Willmottiae*	—	3-pent.gluc.	—	—	—
Poterium obtusum Franch. and Sav.	—	3 : 5-di-	—	—	—
Pyrus Niedzwetzkyana Hemsl.	—	3-mono-	—	—	—
Rosa gallica Linn. var. (Willstätter and Nolan 1915*a*)	—	3 : 5-di-	—	—	—
Rosa polyantha Sieb. and Zucc. vars. (Scott-Moncrieff 1936)	3 : 5-di-	3 : 5-di-	—	—	—
Rubus odoratus Linn.	—	3 : 5-di-	—	—	—

TABLE VI (*cont.*)

DICOTYLEDONS	Pelargonidin	Cyanidin	Malvidin	Delphinidin	Comments
CUNONIALES					
ESCALLONIACEAE					
Escallonia edinensis Hort.	—	3-mono-	—	—	—
GROSSULARIACEAE					
Ribes sanguinem Pursch.	—	3-pent.gluc.	—	—	—
HYDRANGEACEAE					
Hydrangea opuloides Koch. vars.	—	—	—	di-	—
EUPHORBIALES					
EUPHORBIACEAE					
Acalypha hispida Burm.	—	3-mono-A.	—	—	—
Euphorbia fulgens Karw.	—	3-mono-	—	—	—
Poinsettia pulcherrima Grah. (bracts)	—	3-pent.gluc.	—	—	—
MALVALES					
MALVACEAE					
Abutilon insigne Planch.	—	3-pent.gluc.	—	—	—
Althaea rosea Cav. vars.	—	—	3- and di-*	—	*Containing pet. and delph.
Lavatera trimestris Linn. var. *rosea splendens*	—	—	—	*	*Pet.-3-mono-
Malva sylvestris Linn. (Willstätter and Mieg 1915)	—	—	di-	—	—
Malvaviscus Conzattii Greenman	3-bio.	—	—	—	—
Sphaeralcea australis Speg.	3-mono-	—	—	—	—
TILIALES					
STERCULIACEAE					
Sterculia lanceolata Cav.	3-mono-	—	—	—	—
TILIACEAE					
Tricuspidaria dependens Ruiz and Pav.	—	3-bio.	—	—	—
MYRTALES					
MELASTOMACEAE					
Medinilla magnifica Lindl. var. *superba*	—	—	—	di-	—
Tibouchina semidecandra Cogn.	—	—	3 : 5-di-A.	—	—
MYRTACEAE					
Callistemon speciosus DC. (stamens)	—	3 : 5-di-	—	—	—
THEALES					
THEACEAE					
Camellia japonica Linn. and var. "Lady Clare"	—	3-mono-	—	—	—
C. Sasanqua Thunb.	—	3-mono-	—	—	—
CUCURBITALES					
BEGONIACEAE					
Begonia socotrana Hook. f.	—	3 : 5-di-A.	—	—	—

TABLE VI (*cont.*)

DICOTYLEDONS	Pelargonidin	Cyanidin	Malvidin	Delphinidin	Comments
PASSIFLORALES					
PASSIFLORACEAE					
Passiflora racemosa Brot. (petals)	3-mono-	—	—	—	—
(stamens)	—	3-mono-	—	—	—
BIXALES					
CISTACEAE					
Cistus purpureus Lam.	—	—	—	*	*Pet. 3-mono-
Helianthemum nummularium Mill. vars.	—	3-mono-	—	—	—
PITTOSPORALES					
PITTOSPORACEAE					
Sollya heterophylla Lindl.	—	—	—	di-	—
TREMANDIACEAE					
Platytheca galioides Steetz.	—	—	di-A.	—	—
PROTEALES					
PROTEACEAE					
Grevillea punicea R. Br.	—	3-pent.gluc.	—	—	—
THYMELEALES					
THYMELEACEAE					
Daphne cneorum Linn.	—	3-pent.gluc.	—	—	—
LYTHRALES					
LYTHRACEAE					
Lythrum Salicaria Linn. and vars. "Perry", "Crimson Dwarf"	—	—	3 : 5-di-	—	—
ONAGRACEAE					
Clarkia elegans Dougl. vars.	3 : 5-di-	—	3 : 5-di-	—	—
Epilobium angustifolium Linn.	—	—	di-	—	—
E. hirsutum Linn.	—	—	di-	—	—
Fuchsia triphylla Linn.	3 : 5-di-	—	—	—	—
Godetia grandiflora Lindl. var. "Crimson Glow"	—	*	—	—	*Peon. di-
Oenothera Agari Gates	—	3-pent.gluc.	—	—	—
Oe. rubricalyx (calyx) Hort.	—	3-pent.gluc.	—	—	—
Zauschneria californica Presl. var. *latifolia*	3-mono-	—	—	—	—
PUNICACEAE					
Punica granatum Linn. (Karrer and Widmer 1927*b*)	3 : 5-di-	—	—	—	—
GERANIALES					
GERANIACEAE					
Erodium macradenum L'Hérit.	—	—	—	di-*	*Partly methylated
E. Reichardi DC. var. *roseum*	—	—	—	di-	—
Geranium Endressi J. Gay	—	—	3 : 5-di-	—	—
G. grandiflorum Edgw.	—	—	di-	—	—
G. ibericum Cav.	—	—	di-	—	—
G. phaeum Linn.	—	—	—	3-pent.gluc.*	*Partly methylated

TABLE VI (*cont.*)

DICOTYLEDONS	Pelargonidin	Cyanidin	Malvidin	Delphinidin	Comments
GERANIALES (*cont.*)					
GERANIACEAE (*cont.*)					
G. pratense Linn.	—	—	di-	—	—
G. psilostemon Ledeb.	—	—	3 : 5-di-	—	—
G. robertianum Linn.	—	—	di-	—	—
G. sanguineum Linn.	—	—	di-	—	—
Pelargonium cucullatum Ait.	—	—	di-	—	—
P. inquinans Ait.	3-mono-	—	—	—	—
P. peltatum Ait. (Willstätter and Mallison 1915 *b*)	3 : 5-di-	—	—	—	—
P. saniculaefolium Willd.	3 : 5-di-	—	—	—	—
P. Veitchianum Sweet.	—	—	di-	—	—
LINACEAE					
Linum grandiflorum Desf. var. *rubrum*	—	—	—	3-bio.	—
L. narbonense Linn.	—	—	—	di-	—
L. perenne Linn.	—	—	—	di-	—
OXALIDACEAE					
Oxalis rosea Jacq.	—	—	di-	—	—
TROPAEOLACEAE					
Tropaeolum majus Linn. vars.	3-bio.	3-bio.	—	3-bio.	—
POLYGONALES					
POLYGONACEAE					
Polygonum amplexicaule D. Don.	—	3-pent.gluc.	—	—	—
Rumex acetosa Linn.	—	3-bio.	—	—	—
CARYOPHYLLALES					
CARYOPHYLLACEAE					
Dianthus barbatus Linn.	—	3-mono-	—	—	—
D. barbatus vars.	3-mono-	3 : 5-di-	—	—	—
Lychnis chalcedonica Linn.	3-mono-	—	—	—	—
L. Viscaria Linn. var. "Blue Bouquet"	—	—	—	di-*	*Partly methylated
Saponaria vaccaria Linn.	—	3-bio.	—	—	—
Silene angelica Linn.	—	—	di-	—	—
S. Schafta Cmel.	—	3 : 5-di-	—	—	—
SAXIFRAGALES					
CRASSULACEAE					
Crassula coccinea Linn.	—	3-mono-	—	—	—
Kalanchoe coccinea Welw.	—	3-mono-	—	—	—
K. flammea Stapf.	—	3 : 5-di-	—	—	—
Sedum spectabile Bor.	—	—	3-pent.gluc.	—	—
Sempervivum arachnoideum Linn.	—	—	3-pent.gluc.	—	—
SAXIFRAGACEAE					
Astilbe japonica A. Gray var. *purpurea*	—	3-mono-	—	—	—
Bergenia cordifolia A. Br. var. *purpurea*	—	3 : 5-di-	—	—	—
Heuchera sanguinea Engelm.	—	3-bio.	—	—	—
Saxifraga decipiens Ehrh. var. *bathoniensis*	—	3-bio.	—	—	—

TABLE VI (*cont.*)

DICOTYLEDONS	Pelargonidin	Cyanidin	Malvidin	Delphinidin	Comments
POLYGALALES					
POLYGALACEAE					
Polygala amara Linn. (Schmidt and Körperth 1936)	—	—	—	*	*Pet. di-
P. myrtifolia Linn.	—	3 : 5-di-	—	—	—
VIOLALES					
VIOLACEAE					
Viola cornuta Linn.	—	—	—	di-	—
V. gracilis Sibth. and Sm.	—	—	—	di-	—
V. odorata Linn. var. "Princess of Wales"	—	—	—	? sugar A.	—
V. tricolor Linn. var. (Willstätter and Weil 1916)	—	—	—	3-pent.gluc.	—
CRUCIALES					
CRUCIFERAE					
Aethionema grandiflorum Boiss. and Hohen.	—	—	—	3 : 5-di-	—
Aubretia deltoidea DC. vars.	—	3 : 5-di-	—	—	—
Cheiranthus cheiri Linn. vars. (Scott-Moncrieff 1936)	3 : 5-di-	3 : 5-di-	—	—	—
Erysimum linifolium J. Gay	—	3-bio.	—	—	—
Iberis umbellata Linn.	—	3 : 5-di-	—	—	—
Matthiola incana R. Br. vars.	3 : 5-di-A.	3 : 5-di-A.	—	—	—
Orychophragmus violaceus O. E. Schulz.	—	3 : 5-di-	—	—	—
RHOEADALES					
FUMARIACEAE					
Corydalis cava Schweigg and Kört (Schmidt and Körperth 1936)	—	di-	—	—	—
Dielytra spectabilis Don.	—	3-bio.	—	—	—
PAPAVERACEAE					
Eschscholtzia californica, Cham. var. "The Mikado"	—	3-bio.	—	—	—
Meconopsis Baileyi Cotton.	—	3 : 5-di-	—	—	—
M. cambrica Vig. var. fl.pl.	3-bio.	—	—	—	—
Papaver atlanticum Coss.	3-bio.	—	—	—	—
P. nudicaule Linn. vars.	3-bio.	3-bio.	—	—	—
RANALES					
NYMPHAEACEAE					
Nymphaea alba Linn. var. *rubra*	—	—	—	3-mono-	—
N. capensis Thunb. var. *zanzibariensis*	—	—	—	3-mono-	—
N. gigantea Hook.	—	—	—	di-A.	—
N. stellata Willd. var. *odorata*	—	—	—	di-A.	—
RANUNCULACEAE					
Aconitum Napellus Linn.	—	—	—	di-	—
Anemone coronaria Linn. St Brigid vars.	3-bio.	—	—	di-	—
A. fulgens Gay (sepals)	3-mono-	—	—	—	—
(anthers)	—	—	—	di-A.	—

TABLE VI (*cont.*)

DICOTYLEDONS	Pelargonidin	Cyanidin	Malvidin	Delphinidin	Comments
RANALES (*cont.*)					
RANUNCULACEAE (*cont.*)					
A. hepatica Linn. (Schmidt and Körperth 1936)	—	di-	—	—	—
A. Pulsatilla Linn.	—	—	—	di-A.	—
Aquilegia alpina Linn.	—	—	—	di-	—
A. canadensis Linn.	3-mono-	—	—	—	—
A. sibirica Law.	—	—	—	di-	—
Clematis viticella Linn.	—	—	—	3-bio.	—
var. *Kermesina*	—	di-	—	—	—
Delphinium Consolida Linn.	—	—	—	di-A.	—
D. nudicaule Torr. and Gray var. *splendens*	3-bio.	—	—	—	—
Nigella damascena Linn.	—	—	di-	—	—
Paeonia officinalis Linn. var. (Willstätter and Nolan 1915*b*)	—	*	—	—	*Peon. 3 : 5-di-
Ranunculus asiaticus Linn.	—	3-bio.	—	—	—
MAGNOLIALES					
MAGNOLIACEAE					
Michelia fuscata Blume.	—	—	3-pent.gluc.	—	—
MONOCOTYLEDONS					
GRAMINALES					
GRAMINEAE					
Dactylis glomerata Linn. (panicles)	—	3-bio.	—	—	—
ORCHIDALES					
ORCHIDACEAE					
Cattleya labiata Lindl.	—	3 : 5-di-	—	—	—
C. Skinneri Lindl.	—	di-	—	—	—
Masdevallia Harryana Reichb. f.	—	di-	—	—	—
Orchis mascula Linn.	—	3 : 5-di-	—	—	—
Sophronitis grandiflora Lindl.	3-bio.	—	—	—	—
IRIDALES					
IRIDACEAE					
Crocus asturicus Herb.	—	—	—	di-	—
C. hadriaticus Herb.	—	—	—	di-	—
C. longiflorus Rafin.	—	—	—	di-	—
C. nudiflorus Sm.	—	—	—	di-	—
C. pulchellus Herb.	—	—	3 : 5-di-	—	—
C. sativus Linn.	—	—	—	di-	—
C. speciosus Bieb.	—	—	3 : 5-di-	—	—
C. vernus All.	—	—	—	di-	—
Dierama pulcherrimum Baker	—	—	di-	—	—
Iris Kaempferi Sieb. var.	—	—	3 : 5-di-	—	—
I. unguicularis Poir.	—	—	—	di-	—
Ixia speciosa Andr. and var.+	—	3 : 5-di-	—	+*	*Pet. di-

TABLE VI (*cont.*)

MONOCOTYLEDONS	Pelargonidin	Cyanidin	Malvidin	Delphinidin	Comments
AMARYLLIDALES					
AMARYLLIDACEAE					
Agapanthus umbellatus L'Hérit.	—	—	—	di-	—
Allium cyaneum Regel.	—	—	—	di-	—
A. giganteum Regel.	—	3 : 5-di-	—	—	—
A. narcissiflorum Vill.	—	3-mono-A.	—	—	—
Clivia miniata Regel.	3-bio.	—	—	—	—
C. nobilis Lindl.	3-pent.gluc.	—	—	—	—
Haemanthus Katherinae Baker	3-bio.	—	—	—	—
Hippeastrum aulicum Herb.	3-pent.gluc.	—	—	—	—
H. equestre Herb.	3-pent.gluc.	—	—	—	—
Lycoris radiata Herb. (Hayashi 1937)	—	3-mono-	—	—	—
ARALES					
ARACEAE					
Anthurium Scherzerianum Schott.	3-pent.gluc.	—	—	—	—
ALSTROEMERIALES					
ALSTROEMERIACEAE					
Alstroemeria aurantiaca Don.	—	3-bio.	—	—	—
PHILESIACEAE					
Lapageria rosea Ruiz and Pav.	—	3-mono-	—	—	—
LILIALES					
LILIACEAE					
Camassia esculenta Robins	—	—	—	di-	—
Chionodoxa Luciliae Boiss.	—	—	—	di-A.	—
Colchicum autumnale Linn.	—	—	3-bio.	—	—
Fritillaria Meleagris Linn.	—	3-bio.	—	—	—
Gloriosa Rothschildiana O'Brien	—	3 : 5-di-	—	—	—
Hyacinthus orientalis Linn. var. "Queen of the Pinks"	3 : 5-di-	—	—	—	—
var. "King of the Blues"	—	—	—	di-	—
Lilium dauricum Ker-Gawl. var. *erectum*	—	3-pent.gluc.	—	—	—
L. Martagon Linn.	—	3 : 5-di-	—	—	—
L. ochraceum Franch.	—	3-pent.gluc.	—	—	—
L. speciosum Thunb. var. *rubrum* (petals)	—	—	—	*	*Pet. 3-pent. gluc.
var. *rubrum* (anthers)	—	3-pent.gluc.	—	—	—
L. tigrinum Ker-Gawl.	—	—	—	*	*Pet. 3-pent. gluc.
L. umbellatum Hort.	—	3-bio.	—	—	—
Muscari racemosum Mill. (Schmidt and Körperth 1936)	—	—	—	*3-mono-	*Methylated
Scilla non-scripta Hoffm. and Link. and a pink var.*	—	3-bio.*	—	di-	—
Tulipa Fosteriana Hoog.	3-mono-	—	—	—	—
Veltheimia viridifolia Jacq.	—	3 : 5-di-A.	—	—	—
ZINGIBERALES					
CANNACEAE					
Canna indica Linn.	—	3-pent.gluc.	—	—	—

TABLE VI (*cont.*)

MONOCOTYLEDONS	Pelargonidin	Cyanidin	Malvidin	Delphinidin	Comments
ZINGIBERALES (*cont.*)					
MUSACEAE					
Musa basjoo Sieb. and Zucc. (bracts)	—	3-pent.gluc.	—	—	—
STRELITZIACEAE					
Strelitzia reginae Ait. (pistils)	—	—	—	di-	—
BROMELIALES					
BROMELIACEAE					
Billbergia Sanderiana Morr.	—	—	—	di-	—
Vriesia Duvaliana Morr. (petals)	—	—	—	di-	—
(bracts)	—	—	3 : 5-di-	—	—
COMMELINALES					
COMMELINACEAE					
Commelina communis Linn. (Kuroda 1936)	—	—	—	di-A.	—

Not classified on account of the presence of a second component in relatively large amount

Billbergia Sanderiana Morr. (bracts)	Pel. + cyan. di-glyc.
Cestrum purpureum Standley	Pel. + cyan. pent.glyc.
C. Newellii Nichols	Pel. + cyan. pent.glyc.
Cosmos bipinnatus Cav.	Peon. + cyan. + malv. 3-bio.
Lychnis dioica Linn.	Cyan. + delph. di-glyc.
L. Viscaria Linn.	Cyan. + delph. di-glyc.
Papaver Argemone Linn. (petals)	Pel. 3-bio.
(spots)	Cyan. 3-bio.
P. commutatum Fisch. and Mey. (petals)	Pel. + cyan. 3-bio.
(spots)	Cyan. 3-bio.
P. orientale Linn. var. *bracteatum* vars. (petals)	Pel. 3-bio.
(spots)	Cyan. 3-bio.
P. Rhoeas Linn. vars.	Pel. + cyan. 3-bio.
P. somniferum Linn. vars. (petals)	Pel. + cyan. 3-bio.
(spots)	Cyan. 3-bio.

TABLE VII

	Total no. examined	Pelargonidin		Cyanidin		Delphinidin	
		No.	%	No.	%	No.	%
Species	382	71	19	144	38	197	53
Genera	240	57	24	120	50	117	49
Families	78	30	38	54	69	48	62
Orders	50	23	46	40	80	34	68

might expect therefore to find in the Metachlamydeae a preponderance of the biogenetically less simple anthocyanin types.* A comparison of the distributions throughout the Archichlamydeae and Metachlamydeae is shown in Table VIII. Figures based on the number of species are not included, since Table VII and the graph show them to be misleading. The predominance of pelargonidin and delphinidin

* Note that hirsutin and gesnerin are found only in the Metachlamydeae—also carajuretin.

types in the Metachlamydeae as compared with the Archichlamydeae is not due to artificial selection of the material examined, which, as shown by the graphs in fig. 1, only causes appreciable divergence in the species.

TABLE VIII

	Pelargonidin		Cyanidin		Delphinidin	
	Meta.	Archi.	Meta.	Archi.	Meta.	Archi.
	%	%	%	%	%	%
Genera	24	24	45	56	57	41
Families	54	32	71	68	83	54
Orders	67	39	67	89	100	57

The inference to be drawn is that pelargonidin and delphinidin do occur with greater frequency in the more highly developed plants. Moreover, there is no great difference between the distribution of cyanidin throughout the two divisions other than what is to be expected as a result of an increased proportion of the other types in the Metachlamydeae.

Hence the arguments from the data on floral pigmentation coupled with the distribution of the three principal anthocyanidin types and of leuco-anthocyanins and also from the nature of anthocyanin mixtures lead to the same conclusions. There is little doubt that, whatever may be the starting point and intermediary reactions in the biosynthesis of anthocyanins, cyanidin is the aglycone most readily produced by the plant and by the smallest number of stages.

It is possible that certain of the data in Table VI have some phylogenetic significance, although there are obvious limits to the conclusions which may be drawn. For example, the preponderance of cyanidin in the flowers of trees and shrubs in temperate regions is clearly related to morphological characters. On the other hand, the distribution of pelargonidin appears to be associated with climatic rather than morphological distinctions. Nearly all the plants examined whose flowers contain pelargonidin derivatives originate from tropical or subtropical countries. This observation is interesting in view of the fact that blue (generally delphinidin) is considered to be the predominating colour in alpine flora (Cockerell 1891). Flower-colour type may also be controlled by the preference of insects for certain colours. For example, bees are said to be insensitive to red (von Frisch 1937).

ANALYSES OF GLYCOSIDAL TYPES

(1) The majority of anthocyanins are either 3-monosides or 3 : 5-dimonosides. The relative numbers in which these are found are dependent upon the nature of the anthocyanidin. This is true in leaves and fruits as well as in the flowers, but because of the comparative rarity of pelargonidin and delphinidin derivatives in leaves and fruits, flowers only will be considered. The majority of delphinidin diglycosides in

Table VI are not separated into 3-biosides and 3 : 5-diglycosides. However, synthetic investigations have shown that most of them may with confidence be classed as 3 : 5-dimonosides (Robinson and Robinson 1934, p. 1712, § 2). The following figures give for each anthocyanidin the percentage of the genera in which it is present as a 3 : 5-dimonoside, with the reservation that the figure for delphinidin is probably too high for the reason given above. The 3 : 7-dimonoside possibility is not excluded but has not been proved to occur:

Pelargonidin	30 %
Cyanidin	43 %
Delphinidin	90 %

The number of 3 : 5-dimonosides among delphinidin derivatives relative to the proportion in cyanidin and pelargonidin is very striking. We suggest that this is due to the operation of selection resulting from the greater stability of 3 : 5- as compared with 3-saccharides. The susceptibility to oxidation (which causes destruction of colour) is dependent upon the number of hydroxyl groups in the anthocyanidin molecule. The change cyanidin → delphinidin involves the introduction of an extra hydroxyl group and renders the molecule more readily oxidizable. This could be partially counteracted by a change from 3- to 3 : 5-sugar types, and if this occurred selection should operate in its favour. On this basis more 3 : 5-dimonosides are also to be expected, and are actually found, in cyanidin than in pelargonidin derivatives.

(2) The second point arising from the analysis is the possibility that 3-monosides may represent an earlier evolutionary stage than diglycosides. This is, of course, suggested simply by the nature of the three classes; bioside and dimonoside formation resulting from union of a monoside with a second hexose (or pentose) molecule. Autumn leaves, fruits and flowers, with an increasing degree of variability in anthocyanidin, show a decreasing proportion of 3-monosides expressed as a percentage of the total number of genera containing cyanidin* glycosides:

Autumn leaves	83 %	monoside
Fruits	50	,,
Young leaves	31	,,
Permanently pigmented leaves	23	,,
Flowers	26	,,

It may be inferred from these figures that 3-monosides are biogenetically simpler than biosides and dimonosides, though it is noteworthy that in young leaves and permanently pigmented leaves there should be a greater variation in glycosidal type than there is in the nature of the anthocyanidin.

(3) The data on the frequency with which the other sugar types occur in different

* Reference is made only to cyanidin on account of the scarcity of pelargonidin and delphinidin in leaves and fruits.

parts of plants are also of interest. For the reason given previously, only cyanidin saccharides are considered.

3 : 5-*dimonosides*. As is implied by the suggestion concerning selection of 3 : 5-types, the frequency with which these occur bears a close relationship to the importance of anthocyanins as indicated by the degree of variability of the anthocyanin. Permanently pigmented leaves are the only ones which contain a higher percentage of dimonosides than might be expected:

	% 3 : 5-Dimonosides	% 3-Biosides	% 3-Pentose-glycosides
Autumn leaves	5	3	26
Young leaves	9	30	50
Fruits	17	17	22
Permanently pigmented leaves	27	31	19
Flowers	43	17	21

3-*biosides* and 3-*pentoseglycosides* appear to be distributed more or less at random. It should be pointed out that unless great care is taken to remove anthoxanthins and tannins the distribution of a monoside may simulate that of pentoseglycoside. It is possible that the high proportion of pentoseglycosides found in young leaves is partly due to some such cause, as the extracts contained large amounts of impurities from which complete separation was impracticable.

Acylation of anthocyanins has not been considered; it is probably a secondary and possibly a protective process.

Nitrogenous anthocyanins

Pigments of the betanin type (Schudel 1918; Ainley and Robinson 1937) have now been recognized in several genera. In addition to those recorded by Willstätter (see Robinson and Robinson 1932*b*) and in Parts I, II, IV and V of the "Survey of anthocyanins" (Robinson and Robinson 1931, 1932*a*, 1934, with others 1938) there are a number of plants (Weigert 1895; Gertz 1906; Kryz 1920) which were stated many years ago to contain pigments similar to that of *Beta* and differing from ordinary anthocyanins. The colour reactions employed in their identification are in agreement with our own experience of these substances, and they are included in Table IX. In the case of *Fuchsia* berries we do not know what method of identification was employed, but the author states that the pigment was analogous to that of *Beta* and of *Cactus* flowers.

The list is based on Hutchinson's classification (1926) and it is interesting to note that these pigments are limited to five orders. Of these orders, Hutchinson considers that the Caryophyllales, Chenopodiales, Lythrales and Thymeleales are related, but while admitting that there are grounds for associating the Cactales with the Ficoidaceae (Caryophyllales) he places them far apart.

The fact that the nitrogenous anthocyanins are found only in these five orders would in itself have little phylogenetic significance. However, many systematists differ from Hutchinson on morphological grounds in his placing of the Cactales, and taken in conjunction with this the distribution of the nitrogenous anthocyanins indicates that the Cactales are closely related to the Caryophyllales, Chenopodiales, Lythrales and Thymeleales.

TABLE IX. LIST OF PLANTS IN WHICH NITROGENOUS ANTHOCYANINS HAVE BEEN RECOGNIZED

CACTALES

CACTACEAE

Cereus speciosus K. Schum.
C. grandiflorus Mill.
Opuntia sp.
Zygocactus truncatus Schum.

THYMELEALES

NYCTAGINACEAE

Bougainvillaea glabra Choisy
Oxybaphus nyctagineus Sweet. (Gertz 1906)

LYTHRALES

ONAGRACEAE

Fuchsia sp. (berries) (Kryz 1920)

CHENOPODIALES

AMARANTACEAE

Amarantus sp.
Celosia cristata Linn. (Willstätter, see Robinson and Robinson 1932*b*)
C. plumosa Hort. (Ainley and Robinson 1937)
Iresine Herbstii Hook. f.
I. Lindeni Van Houtte (Weigert 1895)

BASELLACEAE

Basella rubra Linn. (Gertz 1906)

CHENOPODIACEAE

Atriplex hortense Linn. (Willstätter, see Robinson and Robinson 1932*b*)
A. litorale Linn. (Gertz 1906)
Beta vulgaris Linn.
Chenopodium virgatum Thunb. (Gertz 1906)
Corispermum canescens Kit. (Gertz 1906)
Kochia trichophylla Stapf var. *Childsii*
Suaeda maritima Dum.

PHYTOLACCACEAE

Phytolacca decandra Linn. (Weigert 1895; Gertz 1906)

CARYOPHYLLALES

FICOIDEAE

Mesembryanthemum nodiflorum Linn. (Gertz 1906)
M. truncatum Thunb. var. *roseum*
Tetragonia crystallina L'Hérit. (Gertz 1906)

PORTULACACEAE

Portulaca grandiflora Hook.

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The authors are indebted to Dr W. B. Turrill and Dr T. A. Sprague of the Royal Botanic Gardens, Kew, for advice in connexion with the classification.

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