INTERSPECIFIC RELATIONSHIPS AND INTRASPECIFIC VARIATION OF *CHENOPODIUM ALBUM* L. IN BRITAIN

I. THE TAXONOMIC DELIMITATION OF THE SPECIES

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Abstract

The critical nature of *Chenopodium* in general and *C. album* in particular is discussed. Much of the confusion appears to be nomenclatural in origin. Evidence is given to show that the inclusion of *C. viride* L. (*C. suecicum* Murr) within the aggregate species *C. album* is unjustified, the resemblance being only superficial. Conversely, the status of *C. reticulatum* as a taxonomic entity distinct from *C. album* is questioned; the two are interfertile, and are separated only by the single plastic character of reticulate as against smooth seed coat, so that it seems more reasonable to account for this variation in terms of seed coat polymorphism within the one species *C. album.*

A. INTRODUCTION

The genus *Chenopodium* [Tourn.] L. comprises over 100 species, most of which are annual weeds of open habitats. Although of cosmopolitan distribution, their greatest development is in temperate regions, with 19 species either native or established in this country. The genus is characterized in general by rather mealy, simple or lobed leaves, alternately arranged, but very variable in shape. Equally variable inflorescences, either spicate, cymose or indeterminate, bear inconspicuous hermaphrodite or gynomonoecious flowers, and the seeds have characteristic testa sculpturings much used in species diagnosis.

Few workers have studied the genus exhaustively, possibly on account of its unattractive appearance. The first post-Linnean treatment of any importance is that of Moquin-Tandon (1840) in his monograph of the family. Mention must also be made of Murr (1904, 1927), who contributed extensively to the taxonomy of the group, especially to that of the *Chenopodium album* complex. By far the most important nomenclatural and taxonomic contributions, however, have been made by Aellen (1918, onwards), whose work, though exclusively orthodox, with little experimental or cytological data, has done much to pave the way for more critical analyses.

Botanists in this country have been particularly indifferent to *Chenopodium.* The only attempt at an intrageneric classification by a British worker is that of Moss (1914), whose segregation of the British species is, however, insufficiently discriminating to merit further attention. Extensive and invaluable collections in the genus were made by Druce (in Herb. Druce, Oxford University), who was particularly interested in alien forms (Hayward and Druce, 1919); but his nomenclature and taxonomy were untrustworthy, and he contributed little that was original other than recognising countless questionable hybrids.

The most extensive recent taxonomic treatment is that of Aellen and Just (1943). Of the 10 sections in the genus they recognise from American material, 4 are represented in Britain. The typical section *Chenopodium* with which we are here primarily concerned, is further subdivided into 4 subsections, on the criterion of seed-coat marking alone. Though this is the only satisfactory differentiating character, it is doubtful whether a classification based thereon does more than provide a convenient pigeon-holing system, since it frequently cuts across apparent relationships in other respects.

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Indeed, the taxonomic confusion still existing in *Chenopodium* is well known, and appears mainly to result from the following difficulties :

1. The abundance of morphologically similar species, separated qualitatively mainly on characters of the seed, often absent in herbarium material.
2. The existence of polymorphism within the limits of many individual species, and of parallel variation between different species, resulting in a confusion of inter- and intra-specific variation patterns.
3. The occurrence of marked phenotypic flexibility, complicating species identification.
4. The erection - often with little foundation - of numerous putative hybrids to accommodate the complicated variation pattern.

The whole situation clearly calls for experimental work to supplement the classical approach, but a short note by Watson (1868), who attempted a few simple growing experiments, is the only example of ' experimental taxonomy ' within the group so far discovered.

The critical nature of the genus as a whole is particularly well exemplified by *C. album*, which has been considered one of the most difficult species (*cf.* Wahl, 1952). Not only is there a serious lack of clear-cut morphological criteria to distinguish it, but it shows particularly well-marked polymorphism at the biotype level and very wide phenotypic plasticity. Moreover, it is reported to hybridize extensively with related species, and the position is further complicated by the reputed existence of different intraspecific chromosome races (Maude, 1940).

The present paper attempts to delimit *C. album* more precisely, in terms of both classical description and new experimental data. Later contributions will be concerned with the cytology of *C. album* and its allies, with the degree of isolation of the species, and with its intraspecific variation pattern.

B. THE TAXONOMIC POSITION OF *CHENOPODIUM ALBUM* IN BRITAIN

The type specimen, a rather depauperate spicate form, resides in the Linnean Herbarium in London. The limits of the Linnean diagnosis have been variously interpreted in the past, and although modern botanists recognise the majority of the British species of *Chenopodium* as taxonomically distinct, there has been some confusion in the nomenclature at the species level. For a long time *C. opulifolium* Schrad. was confused with *C. viride* L. and *C. album* L. (Knuth, 1838, p. 150; but see Aellen, 1940) and, in addition, various workers have included *C. ficifolium* Sm. and/or *C. pratericola* Rydb. (*C. leptophyllum auct. non* Nutt.) within the limits of *C. album* (Bentham, 1858; Moquin-Tandon, in de Candolle, 1849; Moss, 1914).

In the most recent description of the British species (Clapham, Tutin and Warburg, 1952), *C. album* is given the status of an aggregate species, with three segregates : *C. album* L. (*sensu stricto*), *C. viride* L. (*C. suecicum* Murr), and *C. reticulatum* Aell. It is this situation which needs particular clarification here.

1. THE RELATIONSHIP BETWEEN C. ALBUM L. (SENSU STRICTO) AND C. VIRIDE L.

Much of the difficulty in discriminating correctly between these two taxa was caused by a nomenclatural error which was perpetuated for over half a century and has had far-reaching taxonomic consequences. Although the position has been discussed fully by Aellen (1940), a brief review is necessary here, since it concerns not only interspecific differences but the intraspecific nomenclature of *C. album*.

Linnaeus (1753) described the two taxa as separate species, and differentiated between them thus :

C. album : ' *Chenopodium foliis rhomboideo-triangularibus erosis postice integris : summis oblongis, racemis erectis.*'
C. viride : ' *Chenopodium foliis rhomboideis dentato-sinuatis, racemis ramosis subfoliatis.*'

Neither leaf shape nor inflorescence branching are of diagnostic importance, however, and it is impossible to separate these taxa from the Linnean descriptions alone. Later, Moquin-Tandon (1840) introduced the additional diagnostic criteria of leaf colour and seed characters :

C. album : '*pallide viridibus*' and '*semine laevi nitido margine acuto.*'
C. viride : '*glauco vel obscure viridibus*' and '*semine punctulato nitido margine sub-obtuso.*'

Despite this discrimination, many botanists have confused *C. viride* with a cymose variety of *C. album* later described by Koch (1857, p. 524) as *C. album* var. *cymigerum.* Hudson (1798, p. 106) was probably the first post-Linnean worker to make this false equation, and subsequent workers (e.g. Koch, *loc. cit.*; Babington, 1867; Syme, 1868; Murr, 1904; Moss, 1914; Hegi, 1910) largely followed Hudson; even Moquin-Tandon failed to discriminate correctly in his section on the Chenopodiaceae in de Candolle (1849), only 9 years after his earlier monograph describing *C. viride* as a separate species.

TABLE 1

Morphological differences between *C. album* L. (*sensu stricto*) and *C. viride* L. (*C. suecicum* Murr)

	C. album L.	*C. viride* L.
1.	Testa almost smooth with only faint irregular striae.	Testa surface regularly pitted.
2.	Margin of seed sharply keeled.	Margin of seed obtusely keeled.
3.	Inflorescence form variable -spicate, paniculate or cymose.	Inflorescence form invariably cymose.
4.	Leaves, thick, pale green, never glaucous.	Leaves thin, often glaucous.
5.	Diploid chromosome number $2n = 54$*	Diploid chromosome number $2n = 18$*
6.	Anthocyanin often present.	Anthocyanin rarely present.

* See paper II of this series.

C. viride was unequivocally reinstated as a full species distinct from *C. album* by Aellen in 1933. He showed that *C. viride* was equivalent, not to *C. album* var. *cymigerum*, but to a distinct species since described as *C. suecicum* Murr. Nevertheless, there is still considerable confusion, caused not so much now by nomenclatural discrepancies as by insufficient care in determination. The discriminating characters are given in Table 1, and it is clear from this that a removal of *C. viride* from the *C. album* complex is well founded.

2. THE RELATIONSHIP BETWEEN C. ALBUM (SENSU STRICTO) AND C. RETICULATUM AELL.

Whereas the taxonomic delimination of *C. viride* from *C. album* is based on several criteria, with an evident distinction in the field, the segregation of *C. reticulatum* is by no means so clear-cut. In Aellen's original description (1928), there are only two characters concerned, namely '*folia . . . interdum manifeste triloba*' and '*semen magnum . . . in superficie reticulatum i.e. crate venularum ± regulariter quadratarum inductum, area inter venulas ± levi vel tenuiter regulariter granulato scabra.*' The first of these, i.e. the 3-lobed leaves, has since been recognized by Aellen (*in litt.*, 1955) to be inconstant. On the other hand, the impressive, raised, quadrate reticulum on the seed surface is, in its extreme expression, very pronounced and unmistakably distinct from the more or less smooth seed coat of *C. album*; and this character, moreover, was stated to breed true.

Nevertheless, since species of *Chenopodium* can usually be distinguished from one another by at least some other qualitative or quantitative criteria besides testa markings, a taxonomic segregation based on this single character must be questioned. The constancy and genetic isolation of the reticulation needs to be further assessed, the possibility of other associated morphological differences explored, and the distribution of *C. reticulatum* compared with that of *C. album.*

(a) *Seed characters*

(*i*) *Observations on the nature and degree of the reticulation*

Examination of a large number of specimens in the major herbaria and from extensive personal collections made between 1954–6 has revealed that, in any one plant of the *C. album/reticulatum* complex, a gradation may exist from markedly reticulate seeds, with granular-scabrous interfaces, to seeds which are indistinguishable from the smooth, faintly grooved seeds of typical *album* (Fig. 1). Past workers (e.g. Brenan, 1938) have designated plants with a mixture of smooth and reticulate seeds as *C. album* × *reticulatum*, but this presupposes an initial parental segregation. For the purpose of the present investigation, therefore, *C. reticulatum* is used to embrace any plant with at least some seeds reticulate, as against *C. album* with variously sculptured seeds but with a complete absence of the

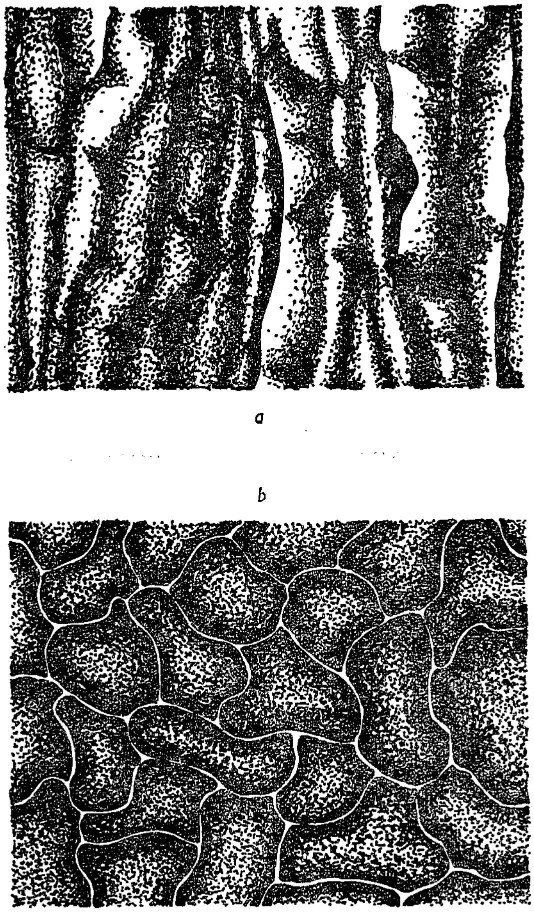

Fig. 1. Surface marking of seeds of (a) *Chenopodium album* and (b) *C. reticulatum.*

raised quadrate reticulum. This arbitrary working separation is perhaps justified by the fact that it is extremely rare to find plants of *C. reticulatum* with uniformly reticulate seeds.

There also exists a parallel series of fainter reticulate markings. These differ in showing a tram-line pattern of two parallel shallow indentations arranged in a reticulate fashion, instead of a raised reticulum. As these markings are relatively inconstant, however, occurring only sporadically in seed samples and not breeding true, they are not considered further here.

The position is further complicated by frequent heteromorphy of the seeds in size and colour. This is a relatively common phenomenon in the genus as a whole, and parallels the situation described for *Atriplex* by Salisbury (1942). In the *C. album/reticulatum* complex occasionally larger, lighter-coloured seeds (mean. wt. *c.* $16{\cdot}07 \times 10^{-4}$ g. as against *c.* $10{\cdot}80 \times 10^{-4}$ g.) may be found in a seed sample, and these rarely show reticulate markings even when the smaller seeds are extremely reticulate. In certain instances, *all* the seeds on a particular plant may be large and light brown, and this may prevent the expression of the reticulation even in what would otherwise be typically reticulate plants.

(*ii*) *Experimental work*

It was obviously necessary to invent a method of recording quantitatively the degree of ' reticulateness ' of individual plants before an experimental analysis of the variation pattern could be undertaken. Four arbitrary grades were therefore delimited, and an index ' α ' derived from these :

$$\alpha = \frac{(1 \times \mathrm{nA}) + (2 \times \mathrm{nB}) + (3 \times \mathrm{nC}) + (4 \times \mathrm{nD})}{\mathrm{N}}$$

where A— D = the four grades in order of increasing distinctness of reticulation
n = the total number of seeds in each class
N = the total number of seeds in the sample.

In spite of various difficulties, such as non-uniformity over different parts of the seed surface, differences in roughness of the seed, and the incidence of extraneous surface punctation, a comparison of replicates within individual samples showed sufficiently close correlation for the method to be used.

α. *Experiment on the washing and drying of seed*

It was frequently noticed that freshly-harvested seed from *C. reticulatum* showed considerably less reticulation than when the same seed was examined later. The ' α ' index was therefore compared on seed :

a. Freshly harvested, with the green perianth and pericarp removed between finger and thumb.
b. Freshly harvested, perianth and pericarp removed as in (a), and the seed then washed in running water.
c. Seed kept dry for > 5 days on top of a 60°C oven, and perianth and pericarp removed when dry.

The results (Table 2) show a progressive increase in the α index in relation to the three treatments. The difference between treatments (a) and (b) is attributed to a film of crushed perianth and pericarp cells obscuring the faint reticulations (subsequently checked on individual seeds) and emphasises the necessity for the seed surface to be thoroughly cleaned when observations are made on fresh material. The increase in the α index under treatment (c), however, suggests that some actual shrinkage of the testa has occurred. Not only must this be taken into consideration in any assessment of seed coat characters, but it also indicates that the degree of reticulation may be, to some extent at least, of a non-genetic nature.

TABLE 2

Changes in the degree of reticulation (α index) in seeds of *C. reticulatum* under different treatments.

Seed Sample	*Value of α index (degree of reticulation)*		
	Freshly harvested seeds	*Freshly harvested seeds ' washed '*	*' Dried ' seeds*
C 1·1	2·50	—	3·73
C 1·3	1·27	3·17	3·50
C 3·2	1·55	—	2·46
C 3·3	1·77	—	2·87
C 3·4	1·63	2·53	2·93
C 5·1	1·23	—	1·50
C 6·1	1·10	1·77	2·50
C 6·4	1·60	—	1·37
A 220·1	—	1·10	3·40
A 220·2	—	1·30	3·67
O 109·1	—	1·63	3·47
O 109·2	—	2·57	3·60
O 109·3	—	1·30	3·23

β. *Controlled growing experiments*

Expt. I. Growth of clones under different external conditions. This experiment was set up to assess the effect of environmental factors on the degree of reticulation in genetically uniform material. Six clones were obtained by cutting individual plants of the *C. album/reticulatum* complex transversely into 5–8 ramets of 1–2 internodes each just after inflorescence initiation, root growth being stimulated by application of M. & B. No. 1 Seradix B to the lower end of each ramet. After a week's growth in sterile ' Vermiculite,' the clones thus obtained were potted out in compost in cool (c. 20°C.), warm (c. 25°C.) and hot (c. 30°C.) greenhouses. Some ramets were enclosed by cellophane-covered frames to ensure inbreeding.

The results of the experiment are given in Table 3. They show considerable variation in the α index within an individual clone, presumably due to environmental conditions, since there appeared to be no correlation between the index value and the original position of the ramet on the individual plant. The plasticity is obviously very great. For example, in Clone C 6, there is a difference in the index between C 6·4 (at 25°C.) and C 6·7 (at 20°C.) of 2·43 units, representing 81% of the total possible variation (i.e. from completely smooth to completely reticulate); even under supposedly uniform conditions (C 6·4 and C 6·3), the variation is 55%.

A comparison of the standard deviation σ of the α index of certain of these results, selected as representing a range of increasingly variable conditions, showed a direct correlation between the value of σ and the relative uniformity of the external conditions. This again suggests that differences in testa markings are at least partly a function of the environment.

Expt. II. Growth of C. reticulatum *under uniform conditions.* Plants from *C. reticulatum* seed collected from 6 different localities were grown together in a cool greenhouse (c. 20°C.), and the seed markings of these F_1 plants compared with those of their parents. The results, given in Table 4, reveal a fairly close positive correlation ($r = +0{\cdot}85$, $P = < 0{\cdot}05$) of the α index between parents and offspring, indicating a considerable measure of genetic control in the extent of seed reticulation. Moreover, the results suggest that the flexibility of expression of seed marking is not as great as might have been assumed from the previous experiment. These differences in result can be partly accounted for by the fact that the temperature in Expt. II approximated more closely to an optimum for growth; this would

TABLE 3

Variation of seed reticulation in clonal material of *C. reticulatum*.
([S] = plant covered with cellophane to ensure self pollination.)

	Ramets						
Clone	1	2	3	4	5	6	7
	Approx. prevailing temperature						
C 1	20°C	—	20°C	—	20°C	20°C	—
C 2	—	—	—	—	[S] 25°C	[S] 25°C	—
C 3	—	[S] 25°C	[S] 25°C	[S] 25°C	[S] 25°C	[S] 25°C	—
C 4	30°C	30°C	20°C	20°C	—	—	—
C 5	20°C	—	—	—	—	20°C	20°C
C 6	20°C	20°C	[S] 25°C	[S] 25°C	—	20°C	20°C
	Degree of reticulation (α)						
C 1	3·73	—	3·50	—	3·03	2·73	—
C 2	—	—	—	—	1·93	1·53	—
C 3	—	2·47	3·00	2·53	2·17	2·70	—
C 4	3·07	2·40	1·60	2·63	—	—	—
C 5	1·50	—	—	—	—	1·87	1·40
C 6	1·77	3·33	2·97	1·37	—	3·47	3·80

tend to increase the heritability of a character by reducing the variance of phenotypic expression.

There is, in addition, a consistent difference between parental and F_1 scores in that the parental seed is generally much more reticulate than that of the F_1 samples. This can be explained on the hypothesis that the temperature differences prevailing during the maturation of the parent and F_1 seed respectively are responsible in such a way that the expression of the reticulateness of the seeds is partly suppressed at higher temperatures; and this is supported by other general observations that material maturing in the field at low temperatures tends to be more reticulate than that grown in warm greenhouses.

TABLE 4

Variation in reticulation (α) of seed coat of parental and F_1 *C. reticulatum*

		F_1 seed			
Seed Sample	*Parental seed*	*Rep.* 1	*Rep.* 2	*Rep.* 3	*Average for F_1*
A	1·53	1·00	1·27	—	1·14
B	1·67	1·27	1·00	1·73	1·33
C	2·23	1·83	1·80	1·67	1·77
D	3·37	1·47	1·80	1·93	1·73
E	3·47	2·47	2·40	—	2·44
F	3·80	3·60	3·07	—	3·34

The two experiments taken together thus suggest that, whereas in nature quite small differences in the degree of seed reticulation may well have a genetic basis, the character is sufficiently plastic to be affected by abnormal environmental conditions.

γ. *Breeding experiments*

Since genetical differences affecting seed reticulation undoubtedly exist between *C. album* and *C. reticulatum*, further experiments were carried out to determine the nature and extent of any genetic isolation between the two.

Expt. I. Controlled reciprocal crosses. The normal emasculation techniques proved quite impracticable for the close-set inflorescences of *Chenopodium*, and the procedure finally adopted was to dust the whole of the young protogynous inflorescence of the selected female parent (previously certified as pollen-free under a binocular microscope) with pollen from the male parent before anthesis of the female parent occurred. Though such a method would obviously be invalid for any quantitative work, it was adequate for a crude indication of crossing ability.

TABLE 5

Results of controlled reciprocal crosses between *C. album* and *C. reticulatum*

Cross ♀ × ♂	*Replicates*	*F_1 seed-marking (No. plants)*		*Percentage crossing*
		At least some seeds reticulate	*Seeds all smooth*	
1. *album* × *reticulatum*	7	5	2	50%
2. *album* × *reticulatum*	5	—	5	
3.* *album* × *reticulatum*	8	5	3	
Control self	7	—	7	
1. *reticulatum* × *album*	21	18	3	22%
2. *reticulatum* × *album*	2	—	2	
Control self	8	4	4	

* Material of *C. album* from Pretoria, S. Africa.

The results of the crosses made are given in Table 5. For the crosses *album* ♀ × *reticulatum* ♂, 50% of the F_1 plants examined showed some evidence of the transfer of genes for reticulateness, in contrast to the selfed *album* control. The results of the reciprocal *reticulatum* ♀ × *album* ♂ cross, however, must be treated with caution, since, although smooth seeds appeared in the F_1 generation, some replicates of the selfed *reticulatum* control exhibited the same phenomenon. This was only to be expected from the nature of the variation of the *reticulatum* character and its possible masking by heteromorphy of the seed (p. 51) and the results as a whole are clearly indicative that at least some gene-interchange between the parental types is possible.

Expt. II. *Field experiment with uncontrolled crossing.* Equal numbers of plants of *C. album* and *C. reticulatum* were planted in four alternate rows, two feet apart, in an experimental plot, and left to set seed by natural means. Examination of the F_1 seed (Table 6) showed that reciprocal intercrossing had occurred between the parental types, while the selfed controls showed no evidence of change in seed coat markings. Even if the evidence from the presumed *reticulatum* ♀ × *album* ♂ crosses is disregarded (see above), the occurrence of c. 10% of reticulate F_1 seeds from the *album* plants not only confirms that gene-interchange may occur in the field, but also gives a minimum measure of the outbreeding potential in nature between the two variants.

TABLE 6

Results of natural cross-breeding in the field between *C. album* and *C. reticulatum*

Maternal parent seed marking	*Plants with F_1 seed marking : Smooth*	*reticulate*
album	9	0
album	10	2
album	4	0
album	4	1
album (control self)	10	0
reticulatum	2	7
reticulatum	0	3
reticulatum	2	14
reticulatum	0	8
reticulatum (control self)	0	5

(b) *Other morphological features*

Five possible morphological *differentiae* were examined, the characters chosen for analysis being those by which at least one other allied species may be either qualitatively or quantitatively distinguished from *C. album* : (i) Inflorescence form, i.e. presence or absence of an intraspecific cymose/spicate variation pattern; (ii) Distribution of anthocyanin, i.e. present as red or purple blotches in the axils of the leaves, restricted to the internodes, diffused through the whole plant, or absent altogether; (iii) Persistence or easy detachment of the pericarp from the seed; (iv) Seed weight; (v) Leaf thickness.

A synopsis of the position for *C. reticulatum* and for 5 other species of *Chenopodium*

TABLE 7

A qualitative comparison of *C. album* with *C. reticulatum* and five other species of *Chenopodium*

Character	*C. reticulatum*	*C. ficifolium*	*C. opulifolium*	*C. variabile*	*C. viride*	*C. berlandieri*
Seed coat marking	S	S	S	S	S	S
Inflorescence	N	S	S	N	S	S
Anthocyanin	N	S	N	S	N	S
Pericarp	N	S	N	S	N	N
Seed weight	N	S	No data	No data	No data	No data
Leaf thickness	N	No data	No data	No data	S	No data
Chromosome No.*	N	S	N	S	S	S
Potential gene* exchange with *C. album*	+	–	–	–	–	–

* Evidence given in later papers.

S = qualitatively separable from *C. album*
N = not qualitatively separable from *C. album*
+ = potential gene exchange possible
– = potential gene exchange improbable.

is given in Table 7; data from chromosome numbers and relative potentiality for gene-exchange (for which the evidence will be given later in papers II and III of this series) have been added to complete the picture. It is clear from this that *C. reticulatum* is indistinguishable from *C. album* by any of the additional criteria here considered, and that a distinction between them is entirely dependent on the very variable reticulation of the seed.

(c) *Distribution and frequency of* C. reticulatum

Since the determination of seed characters requires microscopic examination, which is very rarely made, little is known about the relative distribution of *C. reticulatum* and *C. album* in this country. Of the 12 local floras published since the original description of *C. reticulatum* in 1928, only three (Wolley-Dod, 1937; Good, 1948; Dony, 1953) make any mention of the taxon. However, British herbaria contain much reticulate material included under *C. album*, and this has been supplemented from personal collections. A complete list of the localities and dates of collection of specimens examined showing reticulate seeds is given elsewhere (Cole, 1957), together with similar information from such published references as are available. But the records are so biased by concentration of collecting grounds and by general lack of discrimination in the literature that little reliance can be placed on them as far as general distribution is concerned; all that can be said is that *C. reticulatum* does not appear to possess a markedly different geographical or ecological range in Britain from that of *C. album*.

Nevertheless, an approximate estimate of the relative *frequency* of the *album* and *reticulatum* characters in Britain can be made from the available records if the non-random data from the literature is excluded. Of a total of 661 determinations from actual specimens, the ratio of *album* to *reticulatum* was roughly 9 : 1, showing that, for this country at least, *C. album* appears to be by far the commoner taxon.

Little can be deduced from the available records as to the origin of *C. reticulatum* in this country. Although it was not reported in the literature until 1938 (Lousley, 1938), British herbaria contain much earlier material. The oldest specimen examined, collected from Hastings in 1812, is in the Oxford University herbarium. A comparison of all the material examined in this herbarium with more recent personal collections gives the following relationship :—

	No. sheets examined	*Range of collection dates*	*Identification of specimens*	
			C. album	*C. reticulatum*
Oxford Univ. Herbarium (incl. Druce Collection)	52	1812–1938	78%	22%
Personal collections	347	1954–6	90%	10%

With the exception of one sheet, the Oxford specimens were all collected before *C. reticulatum* was described from Britain and the personal collections were likewise made independently of seed coat pattern, so these numbers may be regarded as comparatively unbiased. They suggest that the incidence of the *reticulatum* character has not changed significantly in recent years.

Extra-British records for *C. reticulatum* are very incomplete. Herbarium material and seed samples received from abroad have produced reticulate specimens from Europe, India and Australia, though similar checking through North American and Canadian material suggests that reticulate seeds are probably absent from that continent so far. Records from France are particularly interesting. From 21 specimens collected from 4 widely scattered localities by a botanist unaware of *C. reticulatum*, 14 possessed reticulate seed coats; there is therefore reason to believe that this variant may be relatively widespread in France, though it is not mentioned in any of the French floras.

C. DISCUSSION

The evidence given in the foregoing pages suggests that *Chenopodium album* L. can no longer be regarded as a critical taxonomic aggregate, and that the status of the three segregates included by Clapham, Tutin and Warburg (1952) under the general heading of *C. album* must now be reassessed. Of these, *C. album* itself (*sensu stricto*) appears on morphological criteria to be a good and easily recognisable Linnean species, as are the other indigenous British *Chenopodia*; although in other countries its variation pattern may be complicated by hybridization, little difficulty has been experienced in determining exact species limits from British material.

The frequent inclusion of *C. viride* in the complex seems to have resulted partly from a superficial resemblance to *C. album* and partly from a persistent nomenclatural confusion in the literature. Close examination of the two, however, has shown that consistent differences can always be detected, particularly in seed coat characters and in the pattern of the inflorescence, and the recognition of *C. viride* as an independent species by Aellen in 1933 is fully supported.

The position to be accorded to *C. reticulatum*, however, is more controversial. Whereas the separation of *C. viride* from *C. album* follows from its recognition as a distinct specific entity (even to the extent of placing it in a separate sub-section of the genus by Aellen and Just in 1943), the removal of *C. reticulatum* as a component of the aggregate involves its degradation to a mere variant of the type species. Since it is indistinguishable from *C. album* in all features except the reticulation of the seed, its taxonomic status must depend on the weight to be attached to this single variable character. Admittedly the reticulation appears to have some genetic basis, and seed coat characters are generally reliable diagnostic criteria in the genus as a whole; but the character is so variable in its expression under different environmental conditions, and so unsupported by other morphological differences, that it seems only reasonable to consider those individuals with reticulate seeds as representing part of a variation pattern within the strict limits of *C. album* itself, a conclusion which is supported by the indications of gene-flow between smooth- and reticulate-seeded plants in the cross-breeding experiments.

Given, however, that the character of reticulate seeds shows quite high heritability, it is of some theoretical interest to consider the way in which intra-individual variation in reticulation may be interpreted. Although xenia (in the sense of Crane and Lawrence, 1947) has been suggested to account for similar variation in other species of *Chenopodium* (Kowal, 1953), this is considered improbable in this case in view of the results of the breeding experiments; these clearly demonstrated that the pollen had no effect upon the seed coat marking of the parental generation but only on the F_1. There is moreover little evidence of differential cytoplasmic influence, so that the only concept remaining is that of individual flexibility arising to a greater or lesser extent as a consequence of ' poor organization ' (Thoday, 1953).

It has already been indicated earlier that individual species of *Chenopodium* frequently exhibit polymorphism. This has been defined by Ford (1940, 1945) as the occurrence of two or more forms of the same species together in the same habitat, and by his definition it is also necessary to show that the existence of the rarest of the forms observed cannot be explained in terms of recurrent mutation. Since, however, even if the form appears in only a small proportion of the population it is very probable that it owes its presence to selection, it is reasonable to assume that the seed coat variation in *C. album* is a true example of polymorphism. Indeed the existence of a large breeding population in this taxon makes it even less likely that mutation pressure alone could account for the observed frequency of reticulate seeds. From the preliminary data given here it is impossible to determine whether the postulated seed-coat polymorphism in *C. album* is transient or balanced. Certainly the distributional data gives no evidence pointing to a recent rapid spread of the reticulate seed-coat genes through the *C. album* population, and this in itself suggests caution in using this character alone to indicate even incipient speciation.

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