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Studies on variation and evolution in *Centaurium erythraea* Rafn and *C. littorale* (D. Turner) Gilmour in the British Isles

1. Taxonomy and biometrical studies

R. A. E. UBSDELL

*Department of Botany, University of Reading**

ABSTRACT

Analysis of populations of *Centaurium erythraea* Rafn subsp. *erythraea* and *C. littorale* (D. Turner) Gilmour subsp. *littorale* has shown that both show a wide range of morphological variation. Much of this variation is retained in cultivation and five varieties are recognized of subsp. *erythraea* and four of subsp. *littorale*. Despite this variation the two subspecies are quite distinct.

Analysis of mixed populations of the two species from the coasts of Anglesey and Lancashire has shown that some plants are, to varying degrees, intermediate and probably of hybrid origin. In the majority of populations from the Lancashire coast, backcrossing to *C. littorale* appears to have taken place, although two suggest backcrossing to *C. erythraea*. This is in contrast to the situation in the population from Anglesey in which only F_1-like hybrids were present. Analysis of two populations from northern Germany show all plants to be intermediate and F_1-like.

INTRODUCTION

The genus *Centaurium* Hill (*Erythraea* Borkh. *nom. illegit.*) of the Gentianaceae is widespread in Europe, especially around the Mediterranean. Taxonomic investigations of the genus have presented great difficulties since the species are extremely variable. Parallel variation in several characters is common in the groups of related species, and there have also been reports of natural hybrids. Species and infra-specific taxa are, therefore, often difficult to define and the literature is full of nomenclatural confusion.

However, Zeltner's work (1970) has led to a better understanding of relationships within the genus. He concentrated primarily on cytological studies, but correlated this with evidence from morphology, ecology and geographical distribution. He showed that in Europe the genus consists of certain ancient, morphologically distinct species, together with a number of taxonomically difficult complexes. It is in the subsections *Parviflorae* (Ronniger) Melderis, *Vulgaria* Melderis and *Centaurium* of the section *Centaurium* that the nomenclature is particularly confusing since the principal species of each, *C. pulchellum* (Sw.) Druce, *C. littorale* (D. Turner) Gilmour and *C. erythraea* Rafn, show parallel variation in many of the characters and numerous subspecies and varieties of each have been described without adequate study.

Subsection *Parviflorae* consists of two annual species, *C. pulchellum* and *C. tenuiflorum* (Hoffmanns. & Link) Fritsch, both of which grow in the British Isles. The former is hypotetraploid ($2n = 36$), while the latter has both diploid ($2n = 20$) and tetraploid ($2n = 40$) races, of which only the diploid is found in the British Isles.

Subsection *Vulgaria* consists of the narrow-leaved, biennial species. Three are diploid ($2n = 20$) and confined to Spain, Portugal and southern France, while another two are tetraploid ($2n = 40$). Of the latter, one is found only in Spain and Portugal, while *C. littorale* is present in central and northern Europe and is the only species of this subsection found in the British Isles. There is a sixth species, confined to Spain and Portugal, for which no chromosome count is available.

Subsection *Centaurium* consists of the broad-leaved, biennial species. One of these is diploid and confined to the Mediterranean region, while *C. erythraea* is the most widespread species of the

* Present address: Botany School, University of Oxford.

genus and is the only one of this subsection present in the British Isles. It has both diploid and tetraploid races, the diploids being confined to the Mediterranean region while the tetraploids have spread into central and northern Europe including Russia and the British Isles. The tetraploids also appear to have been introduced into North America and Australia.

Zeltner's work and Melderis's recent account of the genus for *Flora Europaea* (Melderis 1972a & b) have cleared up much of the nomenclatural confusion surrounding the European species of these three subsections. However, little experimental work has been carried out on the taxa of northern Europe, especially on *C. erythraea* subsp. *erythraea* and *C. littorale* subsp. *littorale*. Both are extremely polymorphic and numerous varieties of each have been described, particularly in the British Isles (Wheldon & Salmon 1925, Gilmour 1937). There is still much confusion over the status of many of these varieties as they are based upon poorly defined characters and given only vague descriptions.

Four varieties of *C. erythraea* subsp. *erythraea* were recognised by Gilmour and named under *C. umbellatum* Gilib. as follows:

i) Var. *centaurium* (L.) Gilmour is the typical, tall variety of the species.

ii) Var. *fasciculare* (Duby) Gilmour is distinguished by its numerous axillary branches (the plant is often as broad as it is tall). It occurs in exposed places on the coasts of Scotland and Ireland.

iii) Var. *subcapitatum* (Corb.) Gilmour is strictly maritime and distinguished by its solitary stem, crowded cauline nodes, compact inflorescence and dwarfness. It has been confused with *C. capitatum* (Willd.) Borbás, a dwarf, maritime plant with the stamens inserted at the base of the corolla-tube. *C. capitatum* was originally treated as a distinct species but is now included in *C. erythraea* subsp. *erythraea* as var. *capitatum* (Willd.) Melderis (Melderis 1972b).

iv) Var. *sublitorale* (Wheldon & Salmon) Druce was thought (Wheldon & Salmon 1925) to be a hybrid between *C. erythraea* and *C. littorale* as it has certain characteristics of both species, but without definite evidence they treated it as a variety of the former.

These varietal names will be used throughout this account since the combinations under *C. erythraea* do not exist, although Melderis (1972b) has shown that the name *C. umbellatum* Gilib. is an invalidly published, nomenclatural synonym of *C. erythraea* Rafn.

Gilmour also recognized four varieties of *C. littorale* subsp. *littorale*. Two from the coasts of north-eastern England and eastern Scotland are glabrous, while the other two from the coasts of North Wales, north-western England and south-western Scotland are scabrid with a dense covering of small papillae on the stem, leaves, bracts and calyx:

i) Var. *occidentale* (Wheldon & Salmon) Gilmour is the common scabrid variety found on the coasts of North Wales, north-western England and south-western Scotland.

ii) Var. *bayleyi* (Wheldon & Salmon) Gilmour is distinguished from the former by its dwarf, much branched habit (the plant is as broad as it is tall), compact inflorescence, longer leaves and larger flowers. It is reported from the coasts of Anglesey and Lancashire.

iii) Var. *littorale* is a dwarf, glabrous variety distinguished by its habit, short calyx and long capsules. It is reported from the coasts of north-eastern England and eastern Scotland.

iv) Var. *minor* (Hartm.) Gilmour is reported from a few places on the coasts of north-eastern England and eastern Scotland, but it is difficult to see how it differs from var. *littorale* except in the lengths of the calyx and capsule.

There have also been reports of hybrids, plants morphologically intermediate between the two species, from mixed populations on the coasts of Lancashire and North Wales, and these add to the confusion.

Wheldon (1897) described in detail the characteristics of some plants which he collected from Hightown, S. Lancashire, v.c. 59 in 1894 (specimens in **BM**). He thought them to be hybrids between *C. littorale* and *C. erythraea* since they had some of the characteristics of both, but named them *Erythraea littoralis* var. *intermedia* Wheldon as they resembled *C. littorale* more closely and were also highly fertile.

Salmon & Thompson (1902) referred to a series of plants collected by them from Ansdell, W. Lancs., v.c. 60 (in **BM**). Some of them were clearly *C. erythraea*, others *C. littorale*, while the rest were intermediate and sterile. They thought that the latter might be hybrids.

Wheldon & Salmon (1925) later described a variety of *C. erythraea* under the name of *Erythraea centaurium* var. *sublitoralis* Wheldon & Salmon from western England and Wales, which they considered to be a hybrid between *C. erythraea* and *C. littorale*. However, without definite evidence of this they treated it as a variety of the former, and the name *C. umbellatum* var. *sublitorale* (Wheldon & Salmon) Druce was later given to it (Druce 1926).

O'Connor (1955) described the results of an investigation of *Centaurium* from the dunes at Freshfield, S. Lancs., v.c. 59 carried out by her in 1954. She found distinct populations of each species, and other populations which contained both species together with plants that could not be referred to either. Vohra (1970) also looked in detail at populations from Freshfield and Ainsdale, S. Lancs., and his results were the same as those of O'Connor.

O'Connor also remarked that plants possessing characters similar to those classed as intermediates in mixed populations from the west coast have been reported from East Anglia, although *C. littorale* is not known there.

A detailed biosystematic study was therefore carried out by the present author to investigate and describe the variation patterns shown by populations of *C. erythraea* subsp. *erythraea* and *C. littorale* subsp. *littorale* in the British Isles and northern Europe. It was hoped that an experimental approach to this problem would both help to reduce some of the taxonomic confusion surrounding the numerous varieties of these two subspecies and explain the nature of the morphologically intermediate plants in mixed populations. This work formed the contents of a thesis accepted for the degree of Ph.D. by the University of Reading (Ubsdell 1973) and will be presented in three papers.

This first paper is concerned with a biometric analysis of morphological characters. The purpose of this study was to assess the extent of the variation in certain morphological characters, and by so doing to delimit the range of variation shown by these two species. This information was then used as a basis for assessing the morphological evidence for hybridization.

An account of the cytology will be given in a second paper, and a final paper will deal with the isolating mechanisms which normally keep these two species distinct in the wild.

TABLE 1. LOCALITIES OF POPULATIONS SAMPLED

Centaurium erythraea	*Centaurium littorale*
1. Kevington, W. Kent, v.c. 16	A. Ainsdale, S. Lancashire, v.c. 59
2. Headley, Surrey, v.c. 17	D. Ainsdale, S. Lancashire, v.c. 59
3. Box Hill, Surrey, v.c. 17	F. Ainsdale, S. Lancashire, v.c. 59
4. Orpington, W. Kent, v.c. 16	G. Ainsdale, S. Lancashire, v.c. 59
5. Folkestone, E. Kent, v.c. 15	H. Ainsdale, S. Lancashire, v.c. 59
6. Luccombe, Isle of Wight, v.c. 10	BA. Newborough, Anglesey, v.c. 52
7. Sandown, Isle of Wight, v.c. 10	N. Newborough, Anglesey, v.c. 52
8. Swanage, Dorset, v.c. 9	24. Holy Island, Cheviot v.c. 68
10. Bonchurch, Isle of Wight, v.c. 10	R. Ross, Cheviot v.c. 68
11. Freshwater, Isle of Wight, v.c. 10	22. Nairn, v.c. 96b
12. Steyning, W. Sussex, v.c. 13	EL. near Elgin, Moray, v.c. 95
13. Bude, E. Cornwall, v.c. 2	T. Tain, E. Ross, v.c. 106
23. Aberlady, Haddington, v.c. 82	DO. Dornoch, E. Sutherland, v.c. 107
25. Newbiggin, S. Northumberland, v.c. 67	
26. Cardiff, Glamorgan, v.c. 41	Mixed populations of the two species
27. Fanore, Clare, v.c. H9	14. Hightown, S. Lancashire, v.c. 59
28. Funshin, S.E. Galway, v.c. H15	15. Freshfield, S. Lancashire, v.c. 59
I. Minsmere, E. Suffolk, v.c. 25	16. Freshfield, S. Lancashire, v.c. 59
J. Minsmere, E. Suffolk, v.c. 25	17. Freshfield, S. Lancashire, v.c. 59
K. Wells, W. Norfolk, v.c. 28	18. Freshfield, S. Lancashire, v.c. 59
L. Cley, E. Norfolk, v.c. 27	19. Freshfield, S. Lancashire, v.c. 59
	20. St Annes, W. Lancashire, v.c. 60
Populations of *C. erythraea* with stamens inserted at the base of the corolla-tube	21. Ainsdale, S. Lancashire, v.c. 59
	AN. Newborough, Anglesey, v.c. 52
29. Freshwater, Isle of Wight, v.c. 10	B, C, E, Ainsdale, S. Lancashire, v.c. 59
30. Freshwater, Isle of Wight, v.c. 10	FAL. Falshöft, Schleswig-Holstein, Germany
	S.P. St Peter, Schleswig-Holstein, Germany

MATERIALS

During the summer months of 1970–72, populations of *C. erythraea* subsp. *erythraea* and *C. littorale* subsp. *littorale* were sampled from many parts of the British Isles and from two localities on the coast of north-western Germany. These consisted of either a single species or mixed populations of both, and the localities are listed in Table 1.

METHODS

The populations of single species were subjected to detailed biometric analyses, and the results compared with those from similar analyses of mixed populations, to determine whether the overlap in variation in the mixed populations was due to variation within the species themselves or to hybridity.

Samples of seed from many of the wild populations were sown in the greenhouse and raised to maturity under uniform conditions. Mature flowering plants were pressed and measured for comparison with the wild plants. Plants of *C. erythraea* subsp. *erythraea* and *C. littorale* subsp. *littorale* from the Continent (northern Europe) were obtained as seeds from Botanic Gardens and raised in the greenhouse, as only two populations (both mixed) were sampled in the wild. Sets of voucher specimens have been deposited in **BM** and **OXF**.

CHARACTERS CHOSEN AND METHOD OF ASSESSMENT

After careful consideration of the characters used by Wheldon & Salmon (1925), Melderis (1932) and Warburg (1962) to distinguish between *C. erythraea* subsp. *erythraea* and *C. littorale* subsp. *littorale* including the numerous varieties of each, the following characters were chosen:

1. *Height of stem*

This was measured vertically from the base of the basal rosette of leaves to the tip of the highest flower.

2. *Habit*

The number of main flowering stems and cauline nodes were noted. The lengths of the internodes were also measured to see if the cauline nodes were well spaced or crowded together, and the following three categories were used for scoring:

a) L = long, internodes >2·5 cm long,
b) M = medium, internodes 1·0–2·5 cm long,
c) S = short, internodes < 1·0 cm long.

3. *Inflorescence*

The total number of cymes present on each flowering stem was scored as follows:

a) M = many, >5 cymes,
b) I = intermediate, 3–5 cymes,
c) F = few, <3 cymes.

The length of the internodes between each cyme in the inflorescence was scored to give an estimate of the relative laxity or compactness of the inflorescence and was scored as follows:

a) L = lax, >2·0 cm long,
b) I = intermediate, 1·0–1·9 cm long,
c) D = dense, 0·5–0·9 cm long,
d) VD = very dense, <0·5 cm long.

4. *Length/breadth ratio of cauline leaves*

This ratio was obtained by dividing the total length of the leaf (in mm) by the greatest breadth. For each plant the first three cauline leaves above the basal rosette of leaves were measured and a mean value obtained.

5. *Shape of cauline leaves*
All cauline leaves could be classified without much difficulty into one of the following categories:
a) Elliptical = leaves short and broad with sides never parallel, an acute apex and 5 prominent veins,
b) Linear = leaves long and narrow with parallel sides, an obtuse apex and 1 prominent vein,
c) Linear-elliptical = leaves intermediate in dimensions but with sides never parallel, an acute apex and 3 prominent veins.

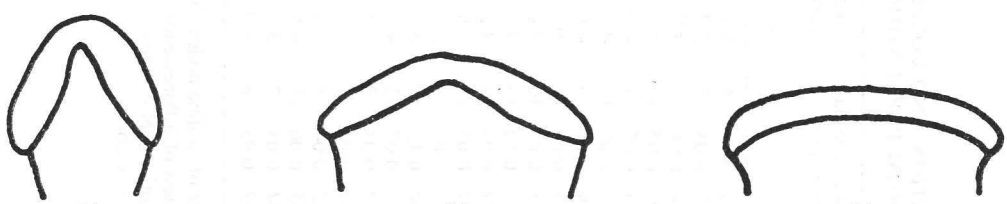
6. *Indumentum*
Plants were scored as follows:
a) Scabrid = margins and midribs of cauline leaves, upper parts of stem, bracts and calyx densely covered in small papillae,
b) Semi-scabrid = all parts lightly covered in papillae,
c) Glabrous = papillae absent.

7. *Calyx/corolla-tube ratio*
This ratio was obtained by dividing the total length of the calyx from the base to the tip of the teeth (in mm), by the length of the corolla-tube. Ten flowers per plant were scored and a mean value obtained.

8. *Length of corolla lobes*
This was measured from the top of the corolla-tube to the tip of the corolla lobes on live material only. Ten flowers per plant were scored and a mean value obtained.

9. *Diameter of the pollen grains*
The pollen grains were mounted in cotton blue/lactophenol and a mean diameter calculated for each plant from 25 grains.

10. *Shape of stigma*
This could be classified into one of three categories:



11. *Length of filaments*
This was measured from their point of attachment to the corolla-tube to the base of the anther.

12. *Length of capsule*

RESULTS

The data derived from the morphological studies can best be considered in three sections:
a) The variation shown by individual characters,
b) An assessment of the overall variation shown by different populations,
c) The correlation of the different characters within individual plants.

VARIATION OF INDIVIDUAL CHARACTERS

For each of the characters studied, the mean, standard deviation and coefficient of variation were calculated for twenty plants in each population. The results are given for populations of *C. erythraea* and *C. littorale* in Tables 2 and 3 respectively, and for mixed populations of the two in Table 4. A comparison of *C. umbellatum* var. *subcapitatum* and *C. erythraea* subsp. *erythraea* var. *capitatum* is given in Table 5.

TABLE 2. MEAN, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR CHARACTERS OF PLANTS FROM POPULATIONS OF *C. ERYTHRAEA*

Population	Height cm			Leaf length: breadth ratio			Calyx:corolla-tube ratio			Length of corolla-lobes mm			Diameter of pollen μm	Habit[1]			Inflores-cence[2]		Leaf-shape[3]	Indum-entum[4]	Stigma-shape[5]
	x̄	s	cv	x̄	s	cv	x̄	s	cv	x̄	s	cv	x̄	(a)†	(b)†	(c)†	(d)†	(e)†			
1	*19·0*	5·6	29	*3·0*	0·29	9·7	*0·56*	0·03	5	*5·3*	0·27	5	26·0	1	5	L	M	D	ELL	G	a
2	*18·6*	7·3	39	*2·7*	0·31	11	*0·57*	0·03	5	*5·2*	0·17	3	26·0	1	5	L	M	D	ELL	G	a
3	*13·3*	2·6	19	*3·0*	0·38	13	*0·54*	0·04	7	*4·9*	0·30	6	25·0	1	5	L	F	D	ELL	G	a
4	*18·5*	4·0	22	*2·7*	0·32	12	*0·50*	0·05	10	*5·5*	0·56	10	25·0	1	6	L	M	D	ELL	G	a
5	*20·8*	7·4	35	*2·8*	0·37	13	*0·55*	0·05	9	*4·9*	0·85	7	25·0	1	5	L	M	D	ELL	G	a
6	*11·2*	6·7	60	*2·1*	0·26	12	*0·50*	0·08	16	*4·5*	0·43	9	25·0	1	4	L	M	D	ELL	G	a
7	*12·0*	4·5	38	*3·0*	0·42	14	*0·59*	0·05	9	*4·9*	0·34	7	24·0	1	5	L	F	D	ELL	G	a
10	*13·7*	3·0	22	*2·6*	0·30	12	*0·49*	0·05	10	*5·4*	0·31	6	25·0	1	4	L	M	D	ELL	G	a
12	*12·6*	3·5	27	*2·9*	0·28	10	*0·51*	0·05	10	*5·4*	0·30	6	25·0	1	5	L	F	D	ELL	G	a
13	*8·0*	10·0	60	*3·0*	0·48	16	*0·56*	0·10	16	*4·5*	0·10	2	25·0	1	4	S	M	D	ELL	G	a
I	*6·8*	1·4	21	*3·1*	0·32	10	*0·53*	0·05	9	*4·5*	0·10	0	24·0	1	4	S	F	D	ELL	G	a
J	*7·5*	2·1	27	*3·5*	0·42	12	*0·44*	0·05	11	*5·0*	0·15	3	25·0	1	5	S	M	D	LIN–ELL	G	a
K	*14·7*	6·9	47	*2·8*	0·45	16	*0·53*	0·04	8	*5·1*	0·15	3	25·0	1	4	L	F	D	ELL	G	a
L	*14·0*	2·6	19	*4·7*	0·45	19	*0·64*	0·12	19	*5·1*	0·11	2	24·0	1	4	L	M	D	LIN–ELL	G	a
8	*4·8*	2·7	16	*2·8*	0·33	12	*0·56*	0·07	12	*4·6*	0·25	5	26·0	1	4	S	M	D	ELL	G	a
27	*6·7*	1·08	16	*2·2*	0·31	14	*0·63*	0·03	5	*4·4*	0·20	5	24·0	1	5	S	M	D	ELL	G	a
28	*14·5*	0·5	1	*2·7*	0·14	5	*0·63*	0·04	6	*5·0*	0·02	3	24·0	1	5	L	F	D	ELL	G	a
23	*5·5*	0·44	25	*2·8*	0·24	9	*0·52*	0·04	8	*4·6*	0·26	6	25·0	6	4	S	M	D	ELL	G	a
25	*16·2*	4·0	25	*3·2*	0·40	13	*0·55*	0·06	11	*4·6*	0·34	7	26·0	1	5	L	M	D	ELL	G	a
26	*30·0*	3·0	25	*2·3*	0·40	17	*0·64*	0·05	7	*5·5*	0·54	10	25·0	1	6	L	F	D	ELL	G	a
Continental	*43·8*	9·3	20	*2·8*	0·34	14	*0·52*	0·05	8	*4·8*	0·34	6	25·0	1	5	L	M	D	ELL	G	a

[1] Habit: †(a) number of flowering stems, †(b) number of cauline nodes, †(c) length of internodes
[2] Inflorescence: †(d) number of cymes, †(e) compactness of inflorescence
[3] Leaf-shape: ELL = elliptic, LIN–ELL = linear-elliptic, LIN = linear
[4] Indumentum: G = glabrous, SS = semi-scabrid, S = scabrid
[5] Stigma-shape: see p. 11.

TABLE 3. MEAN, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR CHARACTERS OF PLANTS FROM POPULATIONS OF *C. LITTORALE* (for abbreviations see Table 2)

Population	Height cm			Leaf length: breadth ratio			Calyx:corolla-tube ratio			Length of corolla-lobes mm			Diameter of pollen μm	Habit[1]			Inflores-cence[2]		Leaf-shape[3]	Indum-entum[4]	Stigma-shape[5]
	x̄	s	cv	x̄	s	cv	x̄	s	cv	x̄	s	cv	x̄	(a)†	(b)†	(c)†	(d)†	(e)†			
A	*6·1*	1·9	25	*5·9*	0·70	12	*0·86*	0·07	8	*5·8*	—	—	30·0	1	3	S	F	L	LIN	S	c
D	*4·1*	0·8	18	*5·6*	0·69	12	*0·83*	0·05	6	*5·9*	—	—	31·0	1	3	S	F	L	LIN	S	c
F	*4·9*	2·6	23	*5·8*	0·52	9	*0·80*	0·06	8	*5·9*	—	—	29·0	1	3	S	F	L	LIN	S	c
G	*5·5*	0·9	17	*5·7*	0·61	11	*0·85*	0·05	6	—	—	—	29·0	1	3	S	F	L	LIN	S	c
H	*6·1*	1·9	31	*5·8*	0·49	8	*0·80*	0·07	9	—	—	—	30·0	1	4	S	F	L	LIN	S	c
N	*5·7*	2·2	39	*7·1*	0·89	13	*0·98*	0·03	3	*6·1*	0·46	8	31·0	1	3	S	F	L	LIN	S	c
BA	*7·0*	2·3	33	*7·6*	0·40	18	*0·97*	0·05	5	*6·6*	0·64	10	30·0	*5*	5	S	F	D	LIN	S	c
24	*4·2*	0·8	20	*5·6*	0·48	9	*0·87*	0·05	6	*5·4*	—	—	29·0	1	1	S	F	L	LIN	SS	c
22	*7·3*	2·2	30	*5·0*	0·41	8	*0·85*	0·05	6	*5·4*	0·27	5	29·0	1	2	S	F	L	LIN	SS/G	c
T	*5·5*	1·6	29	*4·3*	0·83	19	*0·65*	0·10	15	*5·4*	0·42	8	32·0	1	2	S	F	L	LIN	G/SS	c
DO	*3·8*	0·5	13	*4·1*	0·48	12	*0·50*	0·06	12	*4·5*	0·33	7	31·0	1	1	S	F	L	LIN	SS	c
EL	*8·6*	1·9	22	*5·0*	0·54	13	*0·82*	0·12	15	*5·0*	0·44	7	—	1	2	S	F	L	LIN	SS/G	c
R	*4·9*	1·3	26	*5·0*	0·38	8	*0·85*	0·06	5	*5·4*	0·06	5	—	1	1	S	F	L	LIN	SS	c
Continental	*26·8*	6·0	20	*6·3*	0·74	10	*0·81*	0·06	5	*5·9*	0·25	5	30·0	1	3	S	F	L	LIN	G	c

TABLE 4. MEAN, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR CHARACTERS OF PLANTS FROM MIXED POPULATIONS OF *C. ERYTHRAEA* AND *C. LITTORALE* (for abbreviations see Table 2)

Population	Height cm			Leaf length: breadth ratio			Calyx:corolla-tube ratio			Length of corolla-lobes mm			Diameter of pollen μm	Habit[1]			Inflorescence[2]		Leaf-shape[3]	Indumentum[4]	Stigma-shape[5]
	x̄	s	cv	x̄	s	cv	x̄	s	cv	x̄	s	cv	x̄	(a)†	(b)†	(c)†	(d)†	(e)†			
14	*17·3*	4·4	25	*3·9*	1·0	26	*0·82*	0·1	12	*5·6*	0·23	4	24–31	1	5	L	I	L	LIN–ELL	S	b
15	*8·6*	1·6	19	*3·5*	1·1	32	*0·66*	0·15	23	*5·0*	0·28	6	24–29	1	3	S/M	M	D	ELL	G	b
16	*12·3*	3·2	36	*4·8*	0·9	19	*0·77*	0·10	13	*5·3*	0·25	5	26–30	1	3	L	I	L/I	LIN–ELL	S	b
17	*14·0*	4·6	33	*5·1*	1·0	20	*0·77*	0·05	7	*5·2*	0·20	4	30–31	1	4	L	I	L	LIN–ELL	S	b
18	*11·0*	2·1	19	*4·6*	0·62	14	*0·73*	0·07	10	*5·2*	0·20	0	31–32	1	3	L	I	L	LIN–ELL	S	b
19	*12·6*	1·7	20	*3·1*	0·50	16	*0·62*	0·14	22	*5·0*	0·40	8	26–30	1	5	M	M	D	ELL	G	b
20	*16·0*	5·0	31	*4·7*	1·6	34	*0·73*	0·12	16	*5·1*	0·10	2	24–30	1	5	M	I	L/I	LIN–ELL	G	b
21	*18·8*	5·6	30	*4·0*	2·0	50	*0·79*	0·12	15	*5·4*	0·56	10	24–31	1	4	L	I	L	LIN–ELL	S	b
B	*14·0*	4·7	34	*4·5*	1·4	31	*0·80*	0·06	8		—		24–30	1	4	L	F	L	LIN–ELL	S	b
C	*12·5*	3·5	28	*3·7*	1·5	40	*0·70*	0·15	21		—		—	1	4	L	I	L/I	LIN–ELL	S	b
E	*15·3*	8·4	60	*5·3*	1·9	36	*0·74*	0·10	14		—		—	1	4	L	F	L	E/L/L–E	S	b
AN		—			—			—			—		25–30	1	3	L	I	L	E/L/L–E	G	b
FAL	*22·0*	6·6	30	*4·0*	0·4	11	*0·66*	0·05	8	*6·1*	0·21	3	27–28	1	3	L	F	L	LIN–ELL	G	b
S	*17·0*	4·5	26	*4·2*	0·66	12	*0·73*	0·09	12	*5·6*	0·25	4	28	1	3	L	F	L	LIN–ELL	G	b

TABLE 5. MEAN AND STANDARD DEVIATION FOR CHARACTERS OF PLANTS FROM POPULATIONS OF *C. ERYTHRAEA* VAR. *CAPITATUM*, *C. UMBELLATUM* VAR. *SUBCAPITATUM* AND *C. UMBELLATUM* VAR. *CENTAURIUM*

(for abbreviations see Table 2)

Character	*C. umbellatum* var. *centaurium* pop. 5		*C. umbellatum* var. *subcapitatum* pop. 11		*C. erythraea* var. *capitatum* pop. 30		*C. umbellatum* var. *subcapitatum* pop. 29		*C. erythraea* var. *capitatum* pop. 29	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
Height (cm)	*20·8*	5·6	*4·4*	1·0	*1·4*	0·2	*5·8*	2·5	*1·1*	0·2
Habit (a)†(b)†(c)†	1	5 L	1	4 S	1	3 S	1	4 S	1	2 S
Inflorescence	M	D	M	VD	M	VD	M	VD	M	VD
Leaf L/B ratio	*2·8*	7·4	*2·4*	0·3	*2·5*	0·4	*2·9*	0·3	*3·3*	0·2
Leaf-shape	ELL		ELL		ELL		ELL		ELL	
Indumentum	G		G		G		G		G	
Calyx/corolla-tube ratio	*0·55*	0·05	*0·61*	0·06	*1·0*	0·09	*0·79*	0·11	*1·2*	0·17
Corolla-tube length (mm)	*8·7*	0·5	*8·6*	0·6	*4·6*	0·4	*7·3*	1·0	*4·8*	0·7
Corolla-lobe length (mm)	*4·9*	0·9	*5·7*	0·4	*4·7*	0·6	*4·8*	0·7	*4·5*	0·4
Pollen grain diameter (μm)	25·0		25·0		26·0		25·0		26·0	
Stigma-shape	a		a		a		a		a	
Capsule length (mm)	*9·3*	0·8	—	—	—	—	*8·9*	1·1	*6·6*	0·8
Filament length (mm)	*3·3*	0·2	*3·5*	0·7	*5·0*	1·7	*3·4*	0·2	*5·1*	0·6
Point of insertion of stamens	Mouth of tube		Mouth of tube		Base of Tube		Mouth of tube		Base of tube	

1–3. *Height, Habit, Inflorescence*

All three characters are extremely variable and this is to be expected since all are strongly affected by the environment.

a) *C. erythraea*

All plants of this species have 4–6 cauline nodes, and most have a compound inflorescence consisting of many branches each terminating in a compound cyme (more than 5 cymes), although some plants have only 1 or 2 cymes. Populations vary in the length of the cauline internodes, and in the relative laxity/compactness of the inflorescence, and can be divided into three major groups:

i) Populations 1–7, 10, 12, 25, 26, 28, L and K are medium to tall (10–30 cm) with a single main flowering stem, 4–6 cauline nodes, long internodes with well-spaced leaves, and a dense inflorescence of more than 5 cymes, or sometimes only 1 or 2. Plants from populations 1–4, 10, 12, 26 and 28 from inland habitats, 5–7 and 25 from the bases of cliffs by the sea and L and K from pinewoods near sand-dunes, became taller but otherwise retained these characteristics when grown from seed under uniform conditions.

Continental plants grown in the greenhouse resembled the British plants placed in this group.

ii) Populations 8, 11, 13, 27, I and J, together with plants from 29 with normal stamen insertion, are all dwarf (4–8 cm) with a single main flowering stem, 4 or more cauline nodes, short internodes with crowded cauline leaves, and a dense or very dense inflorescence of many (>5) or few (<3) cymes. Plants from populations 27, I and J from sand-dunes became taller and identical to plants in group (i) when cultivated under uniform conditions, whereas plants from populations 8, 11, 13 and 29 from exposed, maritime clifftops retained their original characteristics.

iii) All plants from population 30 and those from population 29 with stamens inserted at the base of the corolla-tube, are even dwarfer (1·1–1·4 cm) with a single main flowering stem, 2–3 cauline nodes, very short internodes with crowded cauline leaves, and a very dense inflorescence of many cymes. These characteristics were retained in cultivation.

iv) Population 23 from sand-dunes is dwarf (4–8 cm) with several main flowering stems (the plant is as broad as it is tall), 4 cauline nodes, short internodes with crowded, cauline leaves, and a dense inflorescence of many cymes. All characteristics were retained in cultivation.

b) *C. littorale*

Plants of this species can be divided into three main groups which, apart from becoming taller, remained constant in cultivation:

i) Populations A, D, F, G and H from sand-dunes on the Lancashire coast and N from Anglesey have one main flowering stem, 3 or 4 cauline nodes (the leaves are longer than the internodes) and a lax inflorescence of few (< 3) cymes.

Continental plants grown in the greenhouse resembled the British plants belonging to this group.

ii) Populations 22, 24, R, EL, DO and T from sand-dunes on the coasts of Northumberland and north-eastern Scotland have one main flowering stem, 1 or 2 cauline nodes with long leaves exceeding the internodes in length, and a lax inflorescence of few (< 3) cymes.

iii) Population BA from sand-dunes on the coast of Anglesey has several main stems (the plant is as broad as it is tall), several crowded, cauline nodes, and a dense inflorescence of few (< 3) cymes. It thus resembles group (iii) of *C. erythraea*.

c) Intermediate plants

These are plants from mixed populations on the coasts of Anglesey and Lancashire which are intermediate between *C. erythraea* and *C. littorale* in a number of characters and cannot be referred to either. These plants are tall (over 10 cm) with 3–6 well-spaced cauline nodes and an intermediate inflorescence of 3–5 cymes.

Many of these characters seem to be adaptations to local environmental conditions and are of little use for separating the two species.

4, 5. *Length/breadth ratio and shape of cauline leaves*

These leaf characters have proved easy to score and are of great use for separating the two species.

a) *C. erythraea*

Plants of this species can be divided into two groups which remained constant in cultivation:

i) The majority of plants have a mean cauline leaf length/breadth ratio falling within the range 2·1–3·3 and elliptical leaves.

ii) Populations J and L have a higher mean leaf ratio with values of 3·5 and 4·7 respectively. These are the narrow-leaved variety with linear-elliptical leaves reported by previous authors from Norfolk and Suffolk.

b) *C. littorale*

Populations of this species show more variation, both within and between populations, although the leaf-shape is linear in all plants. Three main groups can be recognized and all remain constant in cultivation:

i) Populations A, D, F, G and H from the Lancashire coast, 24 and R from Northumberland, 22 and EL from the coast of north-eastern Scotland and plants from the Continent grown in the greenhouse have a mean leaf ratio within the range 5·0–6·3.

ii) Populations BA and N from the coast of Anglesey have a higher mean leaf ratio within the range 7·1–7·6.

iii) Populations DO and T from the coast of north-eastern Scotland have a lower mean leaf ratio within the range 4·1–4·3.

c) Intermediate plants

As all mixed populations in the British Isles occur on the coasts of Lancashire and Anglesey, the value of *C. littorale* is taken to be above 5·0 and that for *C. erythraea* below 3·3. Plants of these two species from the Continent also fall within these values. The leaf ratios of the intermediate plants from the British Isles and Germany fall within the range 3·5–4·8 and the leaves are linear-elliptical. The mean leaf ratios of the mixed populations fall within the range 3·1–5·3.

6. *Indumentum*

a) *C. erythraea*

All populations are glabrous, and this character is retained in cultivation.

b) *C. littorale*

Populations vary in this character and fall into three main groups which remain constant in cultivation.

i) Populations A, D, F, G, H from the Lancashire coast and N from the coast of Anglesey corresponding to var. *occidentale* and population BA from Anglesey corresponding to var. *bayleyi* are densely scabrid.

ii) Populations 22, 24, EL, DO, R and T from the east coast and corresponding to var. *littorale* and var. *minor* are either glabrous or semi-scabrid.

iii) Plants from the Continent are completely glabrous.

c) Intermediate plants

As all plants of *C. erythraea* from single species populations are glabrous and all plants of *C. littorale* from single species populations on the coasts of Lancashire and Anglesey are scabrid, this character can be used to separate them in mixed populations from the British Isles. The intermediate plants vary in this character, as in some mixed populations all are glabrous while in the rest all intermediates are scabrid.

Intermediate plants from mixed populations in Germany were glabrous as are all Continental plants of *C. erythraea* and *C. littorale* subsp. *littorale*.

7. *Calyx/corolla-tube ratio*

This character proved easy to calculate and is one of the best for separating the two species.

a) *C. erythraea*

Populations of this species fall into three main groups:

i) Most have a mean value within the range 0·44–0·59, but this increases in cultivation to 0·64–0·71.

ii) Populations 26, 27, 28 from Wales and western Ireland, plants of this species from mixed populations on the coasts of Lancashire and Anglesey, and population L from eastern Norfolk, have a slightly higher mean value, 0·63–0·64, which increases in cultivation to 0·74–0·76.

iii) Population 30 and plants from 29 with stamens inserted at the base of the corolla-tube have a mean value of 1·0–1·2, which is much higher than that of all other plants of this species. The rest of the plants from population 29 with normal stamen insertion also have a higher mean value of 0·79. Examination of the length of the calyx and corolla-tube shows that the calyx of these plants is of the same length as the calyx of typical *C. erythraea*, and the difference in ratio is the result of the very short corolla-tube of the plants from populations 29 and 30.

b) *C. littorale*

Populations of this species fall into three main groups:

i) Most have a mean value within the range 0·80–0·87, but this increases in cultivation to 0·88–0·97.

ii) Populations N and BA from Anglesey have an even higher value of 0·97–0·98.

iii) Populations DO and T from Sutherland and Ross have a lower mean value of 0·50–0·65. This is atypical of the species and in fact falls within the range of *C. erythraea*.

c) Intermediate plants

Plants of *C. littorale* from the coasts of Lancashire and Anglesey can be clearly separated from plants of *C. erythraea* using this character. Intermediate plants from mixed populations in the British Isles vary with some falling within the range of *C. littorale* from the west coast, others falling within the range of *C. erythraea*, while the rest are intermediate and fall within the range 0·72–0·78. Mixed populations have mean values of 0·66–0·82.

Intermediate plants from Germany have mean values of 0·66–0·73, which is intermediate between the values of Continental plants of *C. erythraea* and *C. littorale*.

8. *Length of corolla lobes*

This character can only be accurately measured on living material.

a) *C. erythraea*

All populations of this species have mean values of 4·4 to 5·5 mm and remain constant in cultivation.

b) *C. littorale*

Populations of this species are more variable and fall into two main groups:

i) Populations from the coasts of Lancashire and Anglesey, and plants from the Continent have mean values within the range 5·8–6·6 mm.

ii) Populations 24, R, 22, EL, DO and T from the east coast have lower mean values within the range 4·5–5·4 mm.

c) Intermediate plants

This character can be used to distinguish plants of *C. littorale* from the coasts of Lancashire and Anglesey from plants of *C. erythraea*. Intermediate plants from mixed populations have mean values within the range 5·4–6·1 mm.

9. *Diameter of the pollen grains*

No mention of this character has been made by previous authors, yet it has proved easy to measure accurately and is of great value in separating *C. erythraea* from *C. littorale*.

a) *C. erythraea*

All plants of this species were found to have pollen grains ranging from 23 to 26 μm with mean values for populations within the range 24–26 μm.

b) *C. littorale*

All plants of this species were found to have larger pollen grains ranging from 28 to 32 μm with mean values for populations within the range 29–32 μm.

c) Intermediate plants

Although some of the intermediate plants from mixed populations have mostly sterile and distorted pollen, most have fertile, spherical pollen grains, like those of *C. erythraea* and *C. littorale*, ranging in diameter from 26 to 30 μm and with population mean values from 27 to 28 μm, which is intermediate between the two species.

10. *Shape of the stigma*

No mention of this character has been made by other authors, yet it has proved easy to score and is of great value in separating living material of the two species. Stigmas of intermediate plants from mixed populations are clearly intermediate in shape between those of the two species.

11. *Length of filaments*

Most plants of *C. erythraea*, and all of *C. littorale* and the intermediates have the filaments ranging in length from 3·0 to 3·8 mm (mean values for populations of 3·3–3·5 mm) and they are inserted at the mouth of the corolla-tube.

All plants of *C. erythraea* from population 30 and some from 29 have the filaments ranging in length from 4·8 to 6·0 mm (mean values for populations of 5·0–5·1 mm) and they are inserted at the base of the corolla-tube.

12. *Length of capsule*

Most plants of *C. erythraea*, and all of *C. littorale* and the intermediates have a similar range (mean values for populations of 8·9–9·3 mm) and the capsules are equal in length to the corolla-tubes.

Plants of *C. erythraea* from populations 29 and 30 with the filaments inserted at the base of the corolla-tube differ. These have shorter capsules (mean value 6·6 mm) which are longer than the stunted corolla-tubes.

SUMMARY OF INDIVIDUAL CHARACTERS

As mixed populations of the two species are found only on the coasts of Lancashire and Anglesey, only the variation shown by plants of *C. littorale* from these areas needs to be considered when selecting characters to distinguish this species from *C. erythraea* in mixed populations from the British Isles. The above analysis of individual characters has shown that the best ones are those listed in Table 6.

TABLE 6. CHARACTERS USED TO DISTINGUISH *C. ERYTHRAEA* FROM *C. LITTORALE* VAR. *OCCIDENTALE* AND VAR. *BAYLEYI*

Character	*C. erythraea*	Intermediate	*C. littorale*
1. Leaf length: breadth ratio	2·1–3·3, short and broad	3·4–4·9, intermediate	5·0–7·6, long and narrow
2. Leaf-shape	elliptic, sides never parallel, 5-veined, apex acute	linear-elliptic, sides never parallel, 3-veined, apex acute	linear with sides parallel, 1-veined, apex obtuse
3. Indumentum	glabrous	semi-scabrid	scabrid
4. Calyx: corolla-tube ratio	0·40–0·64, calyx about half as long as corolla-tube	0·65–0·75, intermediate	0·76–0·98, calyx nearly as long as corolla-tube
5. Corolla-lobe length	4·5–5·4 mm	5·5–5·6 mm	5·7–6·2 mm
6. Diameter of pollen grains	24–26 μm	27–28 μm	29–32 μm
7. Stigma-shape[1]	a	b	c
Score for each	0	5	10
Total hybrid-index score	0	Intermediate	70

[1] See page 11.

AN ASSESSMENT OF THE TOTAL VARIATION SHOWN BY POPULATIONS

To arrive at an assessment of the total variation shown by each plant, a total hybrid-index score was calculated using the characters and numerical scores given in Table 6. Thus, the total hybrid-index score for a plant with all *C. erythraea* characters would be 0 and for a plant with all *C. littorale* characters would be 70. Hybrid-index histograms were constructed to give an indication of the proportion of *C. erythraea*-like, *C. littorale*-like, and intermediate plants present in each population (Figs 1 & 2).

SINGLE SPECIES POPULATIONS OF *C. ERYTHRAEA*

Even in single species populations it can be seen that some plants will have a hybrid-index slightly higher than the theoretical value of 0 (Fig. 1: a–h; Fig. 2: i–m, v). Thus plants with a score of 0, 5, 10 and 15 can be considered to be characteristic of *C. erythraea*.

Plants from the East Anglian populations J (Suffolk) and L (Norfolk) have noticeably higher scores than all other plants of this species (Fig. 2: n & o).

In cultivation, plants of this species range from 0 to 15 (Fig. 2: s) except those from East Anglia, which fall within the range 15–25.

SINGLE SPECIES POPULATIONS OF *C. LITTORALE*

Populations of this species are far more variable in their hybrid-index scores than those of *C. erythraea*.

a) Plants from the coasts of Lancashire and Anglesey have scores of 65–70 (Fig. 1: 1–5; Fig. 2: 7 & 8).

b) Plants from the coasts of Northumberland, Easterness, Moray and those from the Continent grown in the greenhouse, have scores of 50–65, which are slightly lower than the theoretical value (Fig. 1: 6; Fig. 2: 9 & 10, w).

c) Plants from the coasts of E. Ross and E. Sutherland are very different from all other populations of this species since, with values of 30–35 (Fig. 2: 12) and 40–45 (Fig. 2: 11), they fall within the range considered to be intermediate between all other plants of *C. littorale* and *C. erythraea*.

All plants of this species except those from E. Ross and E. Sutherland, which unfortunately were not cultivated, showed scores of 55–70 in cultivation (Fig. 2: t).

MIXED POPULATIONS

The normal range of variation shown by the single species populations does not cause any overlap in the hybrid-index values of the two species, except for plants from E. Ross and E. Sutherland. This is in contrast to the situation shown by mixed populations from the coasts of Lancashire, Anglesey and Germany.

a) Histograms i–vii (Fig. 1) for populations from Hightown, St Annes, Ainsdale, Freshfield and Anglesey all show a broken and uneven transition from *C. erythraea* to *C. littorale*. Obviously there are some plants that are referable to *C. erythraea* with scores of 0–15, and others with scores of 55–70 that are referable to *C. littorale*. The rest are intermediate in a number of characters, and with scores of 20–50 cannot be referred to either.

b) Histograms viii (Fig. 1) and ix (Fig. 2) for other populations from Freshfield show that there are some plants referable to *C. erythraea* and the rest are intermediate.

c) Histograms x and xi (Fig. 2), for other populations from Ainsdale and Freshfield respectively, show some plants referable to *C. littorale* while the rest are intermediate.

d) Histogram xii (Fig. 2) for another population from Freshfield, and x and y (Fig. 2) for German populations show that only intermediate plants are present.

The presence of plants in mixed populations with scores intermediate between those of *C. erythraea* and *C. littorale* is not unreasonable evidence of hybridization.

It is possible that of these intermediate plants those with a score of 25–40 might belong to the F_1 generation, those with scores of 45–50 might be backcrosses to *C. littorale*, and those with scores of 15–20 might be backcrosses to *C. erythraea*. If this is so, it would seem that backcrossing and introgression to *C. littorale* has taken place in population 14 at Hightown (Fig. 1: i), populations 16–19 at Freshfield (Fig. 1: viii; Fig. 2: ix, xi & xii), and in populations 21 and E at Ainsdale (Fig. 1: iii & vi). By contrast, populations 15 from Freshfield and 20 from St Annes (Fig. 1: ii & v) appear to consist of backcrosses to *C. erythraea*.

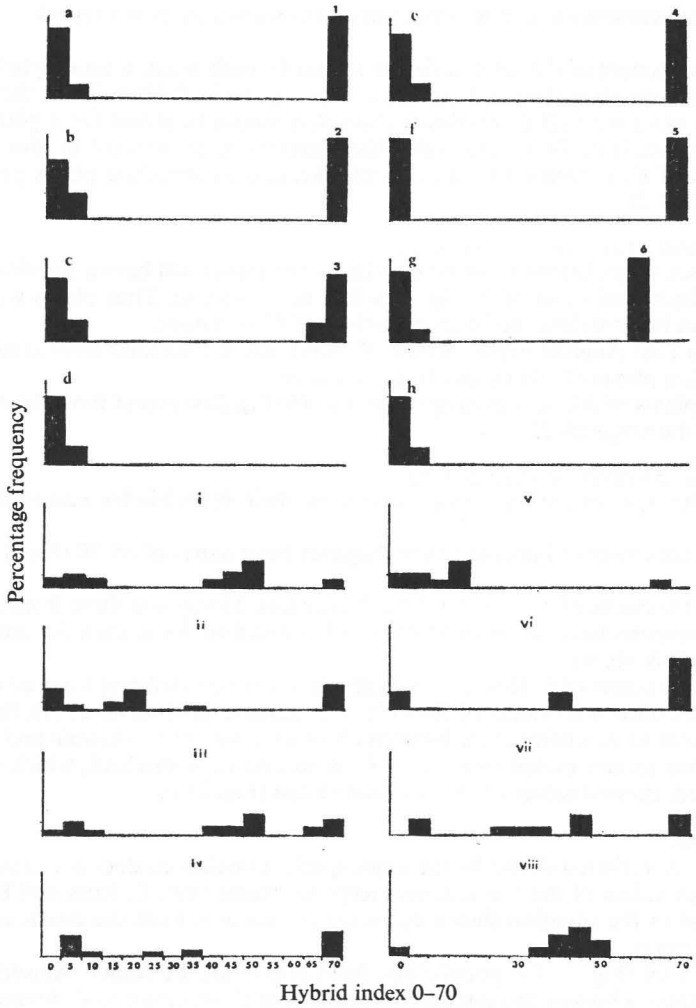


FIGURE 1. Hybrid index histograms.

In populations B and C from Ainsdale (Fig. 1: vii; Fig. 2: x), and those from Anglesey (Fig. 1: iv) and Germany (Fig. 2: x & y) individual plants with scores of 20, 25, 35 and 40 are present

Progeny of intermediate plants grown in cultivation

In cultivation, the progeny of plants from single species populations together with plants of *C. erythraea* and *C. littorale* from mixed populations show hybrid-index values identical to those shown by them in the wild. However, the progeny of intermediate plants from Ainsdale, Freshfielp and Hightown show a variety of intermediate scores (Fig. 2: u). A few had values of 25–30 but the majority ranged from 40 to 50, thus resembling *C. littorale* more closely than *C. erythraea* and strongly suggesting backcrossing to the former species.

THE CORRELATION OF DIFFERENT CHARACTERS WITHIN INDIVIDUAL PLANTS

A more detailed picture of the characters of the individual plants, particularly those of the hybrids, can be seen from pictorialized scatter-diagrams. As space does not allow presentation of all populations examined by this method, only a few representative examples are given.

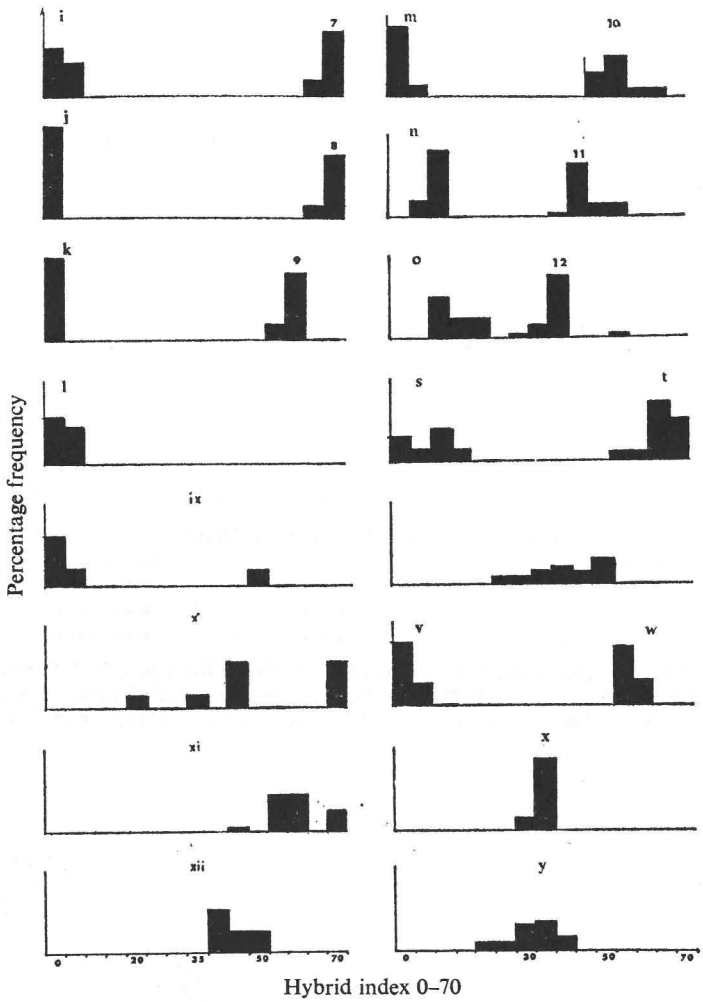


FIGURE 2. Hybrid index histograms. (The unlabelled histogram is u.)

SINGLE SPECIES POPULATIONS OF *C. ERYTHRAEA*

Figs. 3 and 4 show the range of characters found in typical individuals of *C. erythraea* from populations in Surrey (v.c. 17), E. Kent (v.c. 15), Dorset (v.c. 9), Haddington (v.c. 82) and Clare (v.c. H 9). All the characters fall within the range characteristic of *C. erythraea* subsp. *erythraea*.

These studies show that all plants from single species populations of *C. erythraea* subsp. *erythraea*, except those from populations J (E. Suffolk), L (E. Norfolk), 29 and 30 (Isle of Wight), are very similar in most characters, and the only variation is shown by plants from exposed, coastal situations. The three varieties described by Gilmour (1937) under *C. umbellatum* as var. *centaurium*, var. *fasciculare* and var. *subcapitatum* can be recognized, but, as Melderis (1972b) has shown that the correct name for this species is *C. erythraea* Rafn, these three varieties should be placed under *C. erythraea* subsp. *erythraea* as follows:

i) *C. erythraea* subsp. *erythraea* var. *erythraea*
C. umbellatum Gilib. var. *centaurium sensu* Gilmour, *Kew Bull.*, **10**: 497 (1937)

Plants of this variety, the type variety of the species (Melderis 1972b), are tall (9–30 cm high) with a single main stem, 4–6 cauline nodes, long internodes with well-spaced leaves and a dense

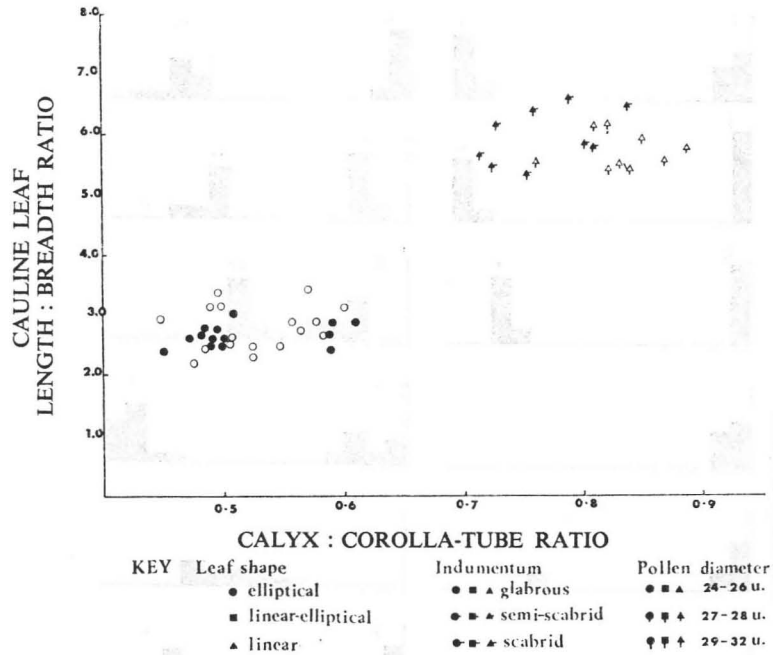


FIGURE 3. Scatter diagram representing populations of *C. erythraea* from Box Hill, Surrey (v.c. 17) (○, pop. 3) and Folkestone, E. Kent (v.c. 15) (●, pop. 5), and populations of *C. littorale* from Ainsdale, S. Lancs. (v.c. 59) (▲, pop. G) and Holy Island, Cheviot (v.c. 68) (△, pop. 24).

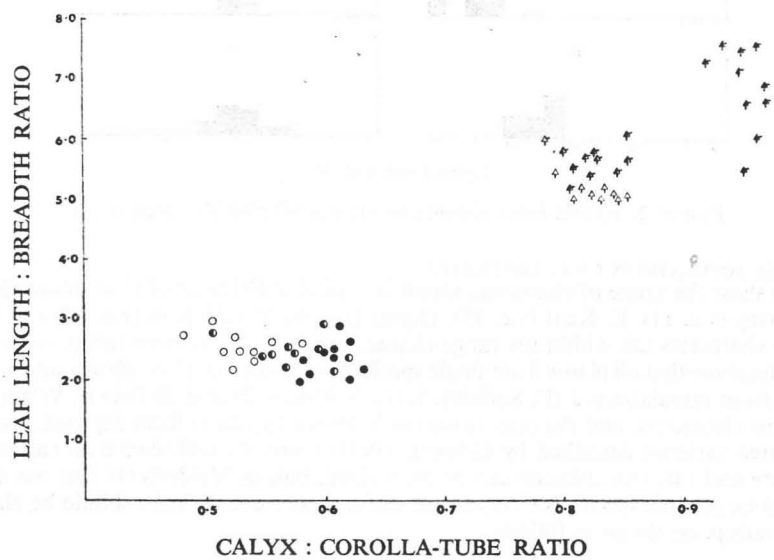


FIGURE 4. Scatter diagram representing populations of *C. erythraea* from Swanage, Dorset (v.c. 9) (◐, pop. 8), Aberlady, Haddington (v.c. 82) (○, pop. 23) and Fanore, Clare (v.c. H9) (●, pop. 27), and populations of *C. littorale* from Newborough, Anglesey (v.c. 52) (▲, pop. BA), Ainsdale, S. Lancs. (v.c. 59) (◭, pop. D) and Nairn (v.c. 96b) (△, pop. 22).

inflorescence of usually at least 5 cymes. It is represented in this study by populations 1–7, 10, 12, 25, 26, 28 and K from inland or sheltered, maritime habitats in parts of southern and northern England, southern Wales and western Ireland, and also by plants from the Continent (northern Europe) raised from seed in the greenhouse.

ii) *C. erythraea* subsp. *erythraea* var. **fasciculare** (Duby) Ubsdell, **comb. nov.**
Chironia centaurium (L.) Curt. var. *fascicularis* Duby, *Botanicon Gallicum*, **1**: 328 (1828)
Erythraea centaurium (L.) Pers. var. *conferta* Wheldon & Salmon, *J. Bot., Lond.*, **63**: 345 (1925)
Centaurium umbellatum Gilib. var. *fasciculare* (Duby) Gilmour, *Kew Bull.*, **10**: 497 (1937)

This usually maritime variety is distinguished by having several main stems, or one main stem and many axillary branches, which often make it as broad as it is tall. It is represented in this study by population 23 from sand dunes on the coast of Haddington (v.c. 82), and in this area is dwarf (4–8 cm) with 4 cauline nodes and short internodes, and each axillary branch terminates in a dense inflorescence of at least 5 cymes. Other much branched, but taller specimens from coastal regions, which retain all these characteristics in cultivation, should be included in this variety.

iii) *C. erythraea* subsp. *erythraea* var. **subcapitatum** (Corb.) Ubsdell, **comb. nov.**
Erythraea centaurium (L.) Pers. var. *subcapitatum* Corbière, *Nouvelle Flore de Normandie*, 392 (1893)
Centaurium umbellatum Gilib. var. *subcapitatum* (Corb.) Gilmour, *Kew Bull.*, **10**: 497 (1937)

This variety is strictly maritime and dwarf (4–8 cm) with 4–6 cauline nodes. It is distinguished from var. *fasciculare* by its solitary, dwarf flowering-stem, extremely short internodes with crowded, cauline leaves, and its very dense, capitate inflorescence of at least 5, crowded cymes. It is represented in this study by populations 8, 11, 13 and plants of population 29 with filaments inserted at the mouth of the corolla-tube. These are all from exposed, maritime cliff-tops in southern England. All its characteristics are retained in cultivation.

Plants of populations 27, J and I from sand dunes in western Ireland and East Anglia resemble this variety, but in cultivation became taller with well-spaced, cauline nodes, and so must be included in var. *erythraea*.

Two other varieties remain to be considered:

iv) *C. erythraea* subsp. *erythraea* var. *capitatum* (Willd.) Melderis (1972b)
Erythraea capitata Willd. in Cham., *Adnot. Fl. Berol.*, 9 (1815)
Erythraea centaurium (L.) Pers. var. b *capitata* (Willd.) Koch, *Synopsis Florae Germanicae et Helveticae*, 492 (1837)

Melderis (1972b) has described this maritime variety as being dwarf with a capitate inflorescence and filaments inserted at the base of the corolla-tube. Although previous authors have treated it as a separate species (*C. capitatum* (Willd.) Borbás), both Zeltner (1970) and Melderis (1972b) considered it to be only a variety of *C. erythraea* subsp. *erythraea* differing from the other dwarf variant (var. *subcapitatum*) only by the level of insertion of the filaments in the corolla-tube. Insertion of the filaments in the basal or middle part of the corolla-tube, instead of at the mouth as is normal for the genus, also occurs in other species of the genus from Europe, and Melderis (1972b) also recognized the following varieties:
C. littorale subsp. *littorale* var. *glomeratum* (Wittrock) Melderis, from the coasts of Sweden, Denmark and Germany, has the filaments inserted at the middle of the corolla-tube.
C. pulchellum var. *morierei* (Corb.) Melderis, known from a single locality on the coast of northern France (Manche), has the filaments inserted in the upper third of the corolla-tube.

Such variants are usually dwarf, with crowded, cauline leaves and a compact inflorescence. They are also rare, being restricted to either a single locality or to a few, small, separate areas, but always within range of their most closely related variety and often growing mixed with it (Jakobsen 1960, Melderis 1972b).

According to Jakobsen (1960) growth of the corolla-tube normally takes place below the insertion of the filaments, but in the above three varieties growth occurs above the insertion of the filaments, or sometimes both above and below it, and the corolla-tube is always stunted in these three. He considered these differences to be of little importance since young buds of all varieties of these three species are identical.

This present study has shown that all plants from population 30 and those from 29 with filaments inserted at the base of the corolla-tube are identical with var. *capitatum* as described by Melderis (1972b). Furthermore, this variety is shown to be similar in most characters to var. *subcapitatum* as both are dwarf, maritime varieties with a single flowering stem, crowded cauline leaves and a very compact inflorescence. Population 29 from exposed, maritime cliff-tops at Freshwater, Isle of Wight, v.c. 10, is in fact a mixture of these two varieties, while population 11 (var. *subcapitatum*) and 30 (var. *capitatum*) were found growing only a few hundred yards away. Plants of var. *capitatum* are shown to differ from var. *subcapitatum* by their more extreme dwarfness (< 2·0 cm), and compactness, by their long filaments inserted at the base of the corolla-tube, and their short, stunted corolla-tubes which equal the calyx but do not enclose the capsules.

All characteristics were retained in cultivation, and observations on floral development support Jakobsen's (1960) observations cited above. I, therefore, agree with Melderis that plants with filaments inserted at the base of the corolla-tube should be given only varietal status as var. *capitatum*.

v) *C. erythraea* subsp. *erythraea* var. **sublitorale** (Wheldon & Salmon) Ubsdell, **comb. nov.**
Erythraea centaurium Pers. var. *sublitoralis* Wheldon & Salmon, *J. Bot., Lond.*, **63**: 346 (1925)
C. umbellatum Gilib. var. *sublitorale* (Wheldon & Salmon) Druce, *Naturalist*, **1926**: 115 (1926)

Wheldon's specimen (**BM**) of this variety, collected in 1921 from Little Sea, Dorset (v.c. 9), is accompanied by a description but it is in fact identical with *C. erythraea* subsp. *erythraea* var. *erythraea* except for its narrower leaves and longer calyx, and does not fit the original description of *Erythraea centaurium* var. *sublitoralis* given by Wheldon & Salmon (1925). Under another narrow-leaved specimen of *C. erythraea* var. *erythraea* collected from St Annes, W. Lancs. (v.c. 60) in 1884 (**BM**) Wheldon has written that this plant comes close to without being identical to his *sublitoralis*, which he considered to be a hybrid between *C. erythraea* and *C. littorale*. Examination of other narrow-leaved plants of *C. erythraea* (**BM**) from S. Hants. (v.c. 11), E. Suffolk (v.c. 25), E. Norfolk (v.c. 27) and W. Norfolk (v.c. 28) by the present author has shown them to be very similar to the plant labelled by Wheldon as var. *sublitoralis* and identical to var. *erythraea* in all other characteristics.

Populations J (E. Suffolk) and L (E. Norfolk) also resemble var. *erythraea* in all characters except for their narrower leaves, which are intermediate in size and shape between those of *C. erythraea* and *C. littorale*, and they are also very similar to Wheldon's plant from Dorset. *C. littorale*, however, is not known south of a line from Northumberland to North Wales, and so it seems unlikely that these narrow-leaved plants from southern England can be of hybrid origin.

Plants from mixed populations on the coast of S. Lancs. (population 15, Freshfield) and W. Lancs. (population 20, St Annes), considered by the present author to be backcrosses to *C. erythraea* var. *erythraea*, resemble the original description of var. *sublitoralis* in most characteristics but not the specimen named by Wheldon as var. *sublitoralis*. It seems, therefore, that Wheldon & Salmon confused plants of hybrid origin from Lancashire with narrow-leaved plants of *C. erythraea* from parts of England from which *C. littorale* is absent. Although the original description of var. *sublitoralis* (Wheldon & Salmon 1925), obviously refers to a hybrid, they do not cite any specimens, and as the only named specimen (**BM**) refers to a narrow-leaved variety of *C. erythraea*, then the name is fixed to the latter. Such narrow-leaved plants of *C. erythraea* from southern England should, therefore, be included under the new combination of *C. erythraea* subsp. *erythraea* var. *sublitorale* (Wheldon & Salmon) Ubsdell and the name cannot be used for plants of hybrid origin.

SINGLE SPECIES POPULATIONS OF *C. LITTORALE*

Figs. 3 & 4 also show the range of characters found in individuals of *C. littorale* from populations on the coasts of S. Lancs. (v.c. 59), Anglesey (v.c. 52), Cheviot (v.c. 68) and Nairn (v.c. 96b). All the characters fall within the range characteristic of *C. littorale* subsp. *littorale*.

These studies show that it is possible to recognize four varieties within this subspecies. Two from the coasts of North Wales, north-western England and south-western Scotland are scabrid, while the other two from the coasts of north-eastern England and eastern Scotland are glabrous.

i) *C. littorale* subsp. *littorale* var. *occidentale* (Wheldon & Salmon) Gilmour (1937)

This is the common scabrid variety found on the coasts of North Wales, north-western England

and south-western Scotland. It usually has a single stem, 3 or 4 cauline nodes, a lax inflorescence of 1 or 2 cymes, and varies in height from 4–12 cm. It is the variety used to represent *C. littorale* in this study in order to distinguish it from *C. erythraea* in mixed populations of the two from the coasts of Anglesey and Lancashire (see Table 6 for other characteristics). It is represented by populations A, D, F, G, H (S. Lancs., v.c. 59) and N (Anglesey, v.c. 52), and is the variety of this species found in all the mixed populations (14–21, B, C, E, AN). All its characteristics were retained in cultivation.

ii) *C. littorale* subsp. *littorale* var. *bayleyi* (Wheldon & Salmon) Gilmour (1937)

This is a second scabrid variety from the coasts of Anglesey and Lancashire. It is distinguished from the former by its numerous flowering-stems and axillary branches, which make it as broad as it is tall, its longer, narrower leaves, longer calyx, larger flowers and more compact inflorescence which is subequalled by long, leaf-like bracts. It is also dwarf (4–8 cm). It is represented in this study by population BA from Anglesey (v.c. 52), but unfortunately it was not grown in cultivation.

The two glabrous (or sometimes semi-scabrid) varieties can also be recognized but their nomenclatural history is confused. *C. littorale* (D. Turner) Gilmour was based on *Chironia littoralis* D. Turner described by Turner (1805) from material collected by Winch in Cheviot (Holy Island and sea coast near Hartley and Bamburgh Links). Melderis (1972b) chose as the lectotype of *Chironia littoralis* a specimen ex Herb. Hooker from Holy Island from Winch's material (**BM**) which agreed with the original description. Gilmour's var. *minor* agrees with typical material of *Chironia littoralis* as exemplified by Winch's specimen, and he used var. *littorale* for the rather atypical form of *Chironia littoralis* from north-eastern Scotland, the first name for which is *Erythraea turneri* Wheldon & Salmon (1925). The nomenclature of these two varieties is, therefore, as follows:

iii) *C. littorale* subsp. *littorale* var. *littorale*

Chironia littoralis D. Turner in Turner & Dillwyn, *Botanists' Guide*, **2**: 469 (1805)

Erythraea littoralis (D. Turner) Fries var. *minor* Hartmann, *Handbok Skandinaviens Flora*, **101** (1820)

Erythraea compressa Hayne var. *friesii* f. *minor* (Hartm.) Wheldon & Salmon, *J. Bot., Lond.*, **63**: 349 (1925)

C. littorale (D. Turner) Gilmour var. *minor* (Hartm.) Gilmour, *Kew Bull.*, **10**: 499 (1937)

This is the typical glabrous or semi-scabrid variety from the coasts of north-eastern England (Cheviot, v.c. 68) and eastern Scotland (Moray, v.c. 95, and Nairn, v.c. 96b), and is distinguished from the two scabrid, west coast varieties (Table 6) mainly by its lack of scabridity but also by its shorter, broader leaves (ratio 5·0–5·6) fewer cauline nodes (1 or 2), smaller flowers and more compact inflorescence. It ranges in height from 4 to 11 cm, and Wheldon & Salmon (1925) placed the taller plants, including those from the Continent (northern Europe), under *Erythraea compressa* Hayne var. *friesii* Wheldon & Salmon, and the smaller plants, notably those from Holy Island on which *Chironia littoralis* was based, under *E. compressa* var. *friesii* forma *minor*. However, apart from the variation in height, they are identical and should be included as a single variety (var. *littorale*). This variety is represented in this study by populations 24 and R (Cheviot), 22 (Nairn) and EL (Moray), and also by plants from elsewhere in northern Europe raised from seed in the greenhouse.

iv) *C. littorale* subsp. *littorale* var. **turneri** (Wheldon & Salmon) Ubsdell, **comb. et stat. nov.**

Erythraea turneri Wheldon & Salmon, *J. Bot., Lond.*, **63**: 347 (1925)

Chironia littoralis D. Turner in Turner & Dillwyn, *Botanists' Guide*, **2**: 469 (1805) *pro parte*

Erythraea littoralis (D. Turner) Fries, *Novitiae Florae Suecicae*, 29 (1814) *pro parte*, auct. angl.

Erythraea vulgaris (Rafn) Wittr. var. *littoralis* (D. Turner) Wittrock, *Bot. Not.*, **1884**: 115 (1884) *pro parte*

Centaurium turneri (Wheldon & Salmon) Druce, *Naturalist*, **1926**: 115 (1926)

C. littorale (D. Turner) Gilmour var. *littorale sensu* Gilmour, *Kew Bull.*, **10**: 499 (1937)

This second glabrous or sometimes semi-scabrid variety has a rather distinct habit, being dwarf (3–6 cm) with a persistent basal rosette of leaves and usually only a single, cauline node. It is distinguished from var. *littorale* mainly by its shorter, broader leaves (ratio 4·1–4·3), shorter non-attenuated sepals (calyx:corolla-tube ratio 0·50–0·65), its shorter but very distinctive concave,

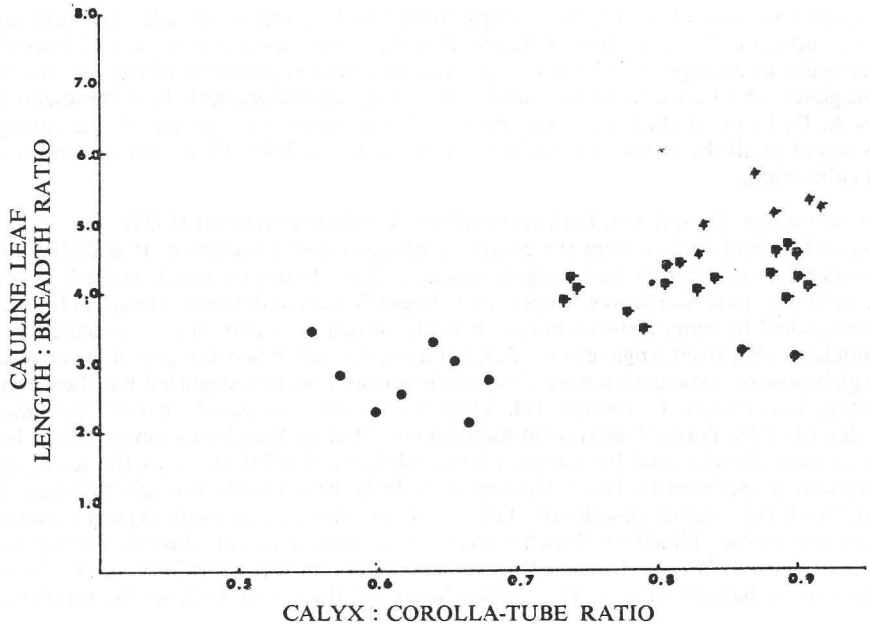


FIGURE 5. Scatter diagram representing a mixed population of *C. erythraea* and *C. littorale* from Hightown, S. Lancs. (v.c. 59) (pop. 14).

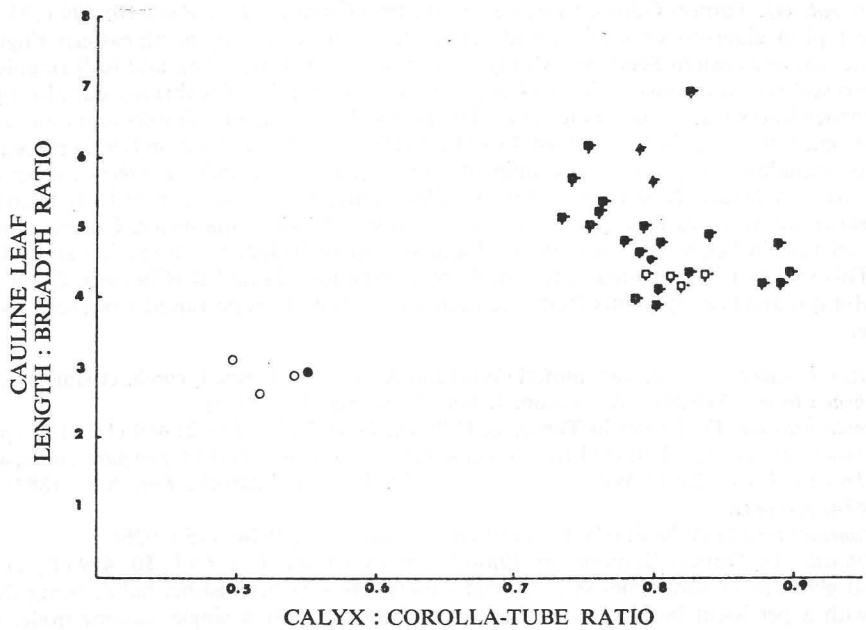


FIGURE 6. Scatter diagram representing two mixed populations from Freshfield, S. Lancs. (v.c. 59) (hollow symbols pop. 18, solid symbols pop. 19).

almost cup-shaped corolla-lobes, and its capsules, which are 2–3 times the length of the calyx, instead of equalling it as in all other varieties of *C. littorale*. It is represented in this study by populations T (E. Ross, v.c. 106) and DO (E. Sutherland, v.c. 107). It is also represented by all other material of this species examined from these localities, and by all plants of this species from Golspie (E. Sutherland) and Munlochy (E. Ross), and by some plants from Campbelltown (Nairn) and Findhorn (Moray).

It is rather different from all other varieties of *C. littorale* as it resembles *C. erythraea* in the calyx:corolla-tube ratio and length of the corolla-lobes, and is intermediate between the two species for leaf length:breadth ratio. Its status is difficult to decide as *C. erythraea* is absent from this part of Scotland, but as it most resembles *C. littorale*, and as plants of var. *littorale* from the coasts of north-eastern England and eastern Scotland have shorter leaves, shorter calyx and smaller flowers than the west coast varieties, it should be included in *C. littorale* as a variety.

MIXED POPULATIONS OF *C. ERYTHRAEA* AND *C. LITTORALE*

Figs. 5–9, representing mixed populations from the coasts of S. Lancs. (v.c. 59), W. Lancs. (v.c. 60) and Anglesey (v.c. 52), show typical plants of both *C. erythraea* and *C. littorale* var. *occidentale*, while the rest are intermediate.

Fig. 10, representing two populations from northern Germany, shows all plants to be intermediate in most characters between *C. erythraea* and *C. littorale* var. *littorale*.

Careful examination of the combinations of intermediate characters found in the natural hybrids shows that most of the plants can be placed under one of several types (Table 7):

a) By far the commonest hybrid plant is that represented by type 1 (Hybrid-index 45–50), to which belong nearly all the hybrids from populations 14 (Hightown), 16–19 (Freshfield) and 21 Ainsdale), and a few from B and C (Ainsdale). It is possible that these plants are backcrosses to *C. littorale*.

b) All hybrid plants from populations 15 (Freshfield) and 20 (St Annes) belong to type 2 (Hybrid-index 15–20), and it is possible that these are backcrosses to *C. erythraea*.

TABLE 7. TYPES OF NATURALLY OCCURRING HYBRID PLANTS

Hybrid-type	Characters of *C. erythraea*	Characters Intermediate	Characters of *C. littorale*	Populations in which present	Hybrid-index
1	—	Leaf characters, length of corolla-lobes, stigma, pollen	Scabridity, calyx/corolla-tube ratio	14, 16, 17, 18, 19, 21, B, C	45–50
2	Scabridity, length of corolla-lobes, stigma, pollen	Leaf characters, calyx/corolla-tube ratio	—	20	15–20
3	Leaf characters	Stigma, pollen	Scabridity, floral parts	B, C, 14	40
4	Leaf characters, scabridity	Stigma, pollen	Floral parts	C	35
5	Floral parts	Leaf characters, stigma, pollen	Scabridity	C	30
6	Scabridity	Leaf characters, stigma, pollen	Floral parts	AN	40
7	Scabridity, floral parts	Leaf characters, stigma, pollen	—	AN	25
8	Stigma	Leaf characters, scabridity, pollen	Floral parts	16, 20	35
9	—	Leaf characters, floral parts, stigma, pollen	Scabridity	17, E	40
10	Leaf characters, scabridity	Floral parts, stigma, pollen	—	B	25
11	—	All characters	—	FAL, SP	25–40

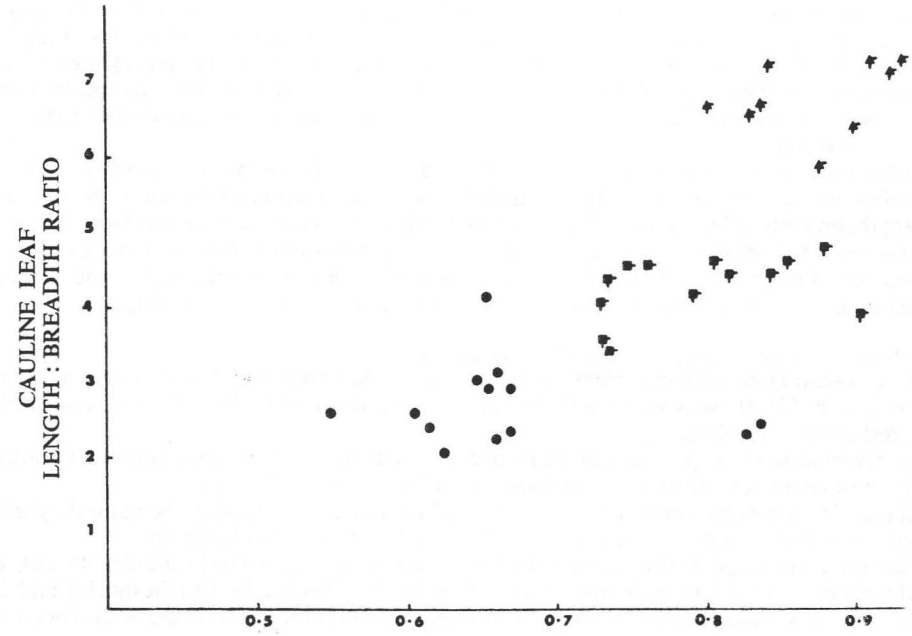


FIGURE 7. Scatter diagram representing a mixed population from Ainsdale, S. Lancs. (v.c. 59) (pop. 21).

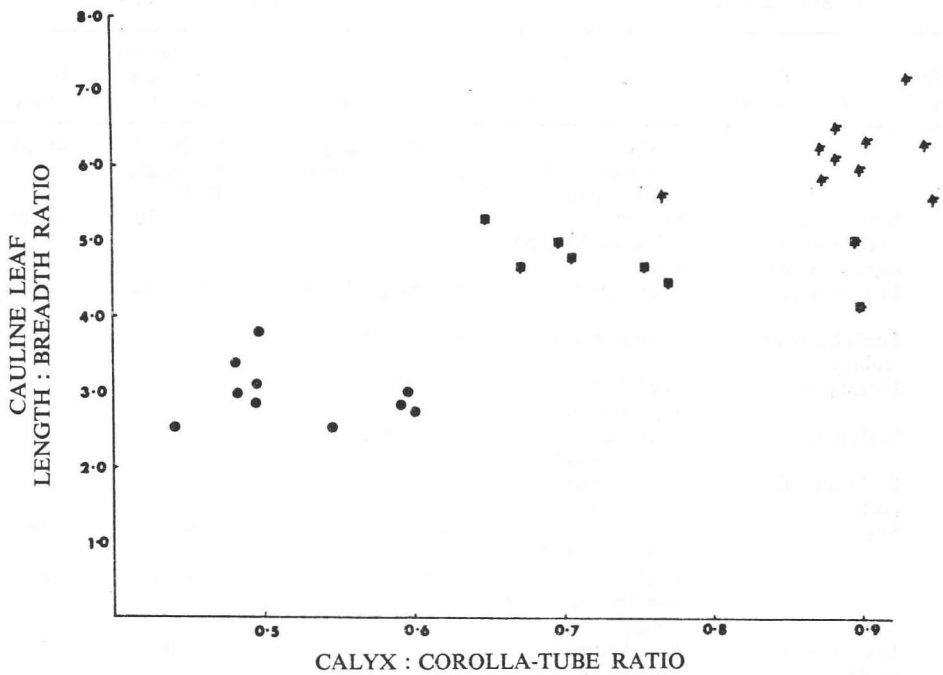


FIGURE 8. Scatter diagram representing a mixed population from St Annes, W. Lancs. (v.c. 60) (pop. 20).

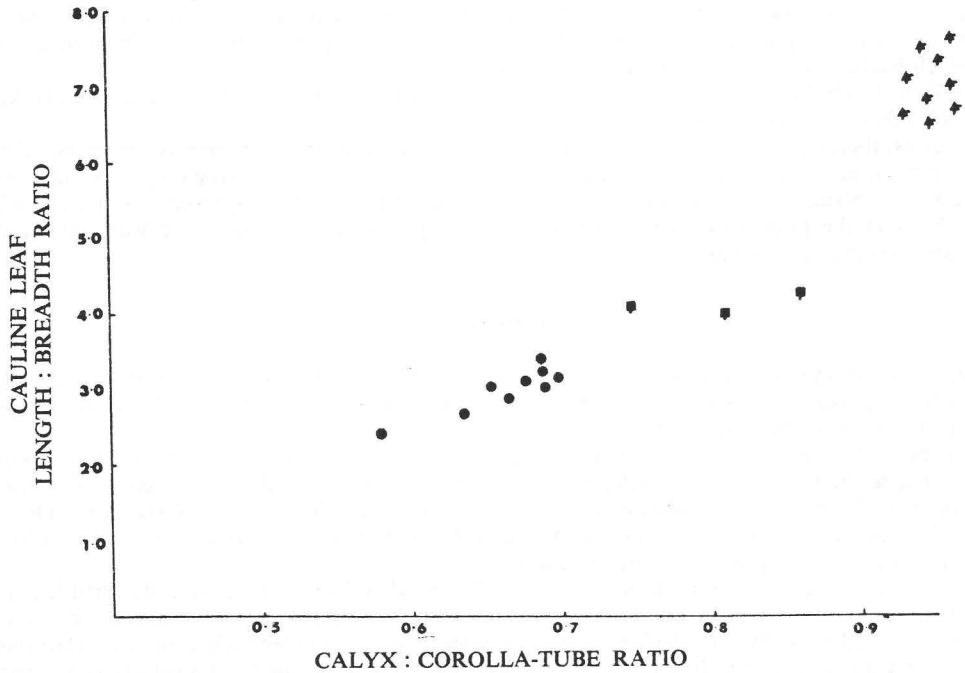


FIGURE 9. Scatter diagram representing a mixed population from Newborough, Anglesey (v.c. 52) (pop. AN).

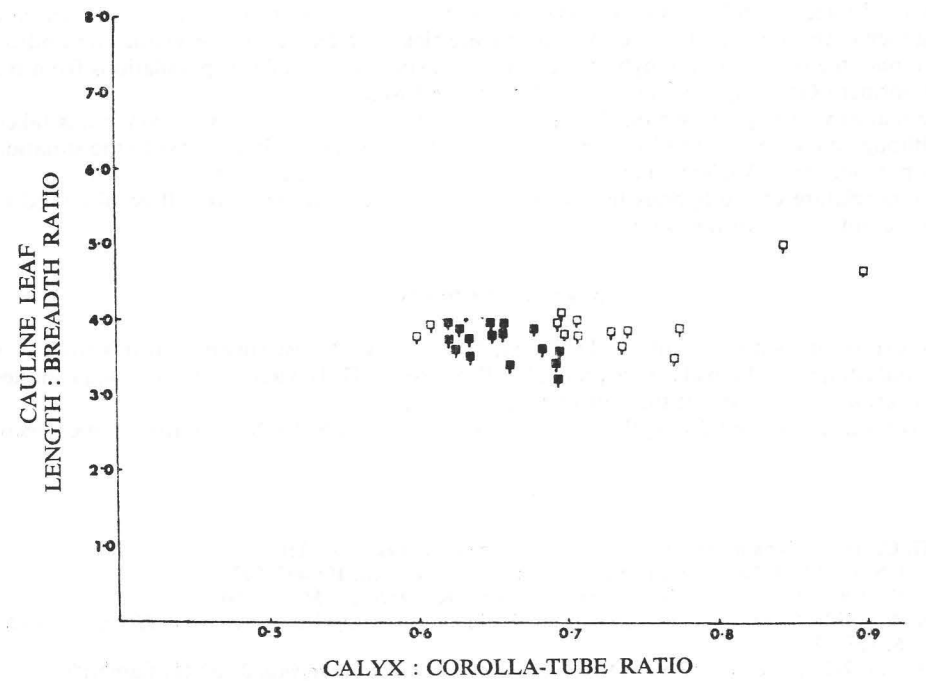


FIGURE 10. Scatter diagram representing two populations from Falshöft (solid symbols) and St Peter (Schleswig-Holstein) (hollow symbols).

c) Types 3–10 (Hybrid-index 25, 30, 35, 40) are represented by a few individuals present in many of the mixed populations from the British Isles. Many appear F_1-like, and, in populations in which backcrosses predominate, they merge with them.

d) Type 11 (Hybrid-index 25–40) is represented by all plants from the two populations (FAL. and S.P.) from northern Germany, and they are F_1-like.

It seems, therefore, that on the Lancashire coast backcrossing to *C. littorale* is commoner than to *C. erythraea*. Neither seems to have happened in the population from Anglesey, in which only three F_1-like plants were found amongst a large number of plants of *C. erythraea* and *C. littorale*. All plants in the populations from northern Germany were F_1-like and there were no plants referable to either of the parental species.

SUMMARY

Morphological analysis of single-species populations of *C. erythraea* subsp. *erythraea* and *C. littorale* subsp. *littorale* has shown that both show a wide range of morphological variation, most of which is retained in cultivation.

It is possible to recognize five varieties of *C. erythraea* subsp. *erythraea* from the British Isles. They include the two named by Melderis (1972b) as var. *erythraea* and var. *capitatum*, and three others to be known as var. **subcapitatum** (Corb.) Ubsdell, **comb. nov.**, var. **fasciculare** (Duby) Ubsdell, **comb. nov.** and var. **sublitorale** (Wheldon & Salmon) Ubsdell, **comb. nov.**, all of which were included by Melderis in his var. *erythraea*.

It is also possible to recognize four varieties of *C. littorale* subsp. *littorale* from the British Isles, all of which were included in var. *littorale* by Melderis (1972b). Two are the scabrid, west coast varieties named by Gilmour (1937) as var. *occidentale* and var. *bayleyi*, while the two glabrous, east coast varieties are var. *littorale* (*sensu* Melderis 1972b) and var. **turneri** (Wheldon & Salmon) Ubsdell, **comb. et stat. nov.**

Despite this variation the two species can be clearly distinguished on the basis of a number of characters.

Analysis of mixed populations of *C. erythraea* and *C. littorale* from the coasts of Lancashire and Anglesey have shown that, while some plants are clearly referable to *C. erythraea* and others to *C. littorale*, the remainder are hybrids between the two. Analysis of two populations from the coast of northern Germany have shown all plants to be F_1-like.

In the majority of populations on the Lancashire coast backcrossing to C. *littorale* has taken place, although backcrossing to *C. erythraea* has also occurred. This is in contrast to the situation in the population from Anglesey, in which only F_1-like hybrids were present.

The nomenclature of the hybrids has been confused in the literature and will be discussed in detail in the third paper of this series.

ACKNOWLEDGMENTS

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