

THE BRITISH FORMS OF *TUBERARIA GUTTATA* (L.) FOURREAU

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ABSTRACT

An account is given of the variation in British *Tuberaria guttata*, and of its previous taxonomic treatment: the taxonomic value of various characters is examined. Most of the Welsh and Irish plants including the type population of *Helianthemum breweri* Planch. differ from *T. guttata* as it occurs in the Channel Isles and northern France in their shorter stature, the more common presence of bracts and other characters. All the characters said to distinguish *breweri* intergrade continuously with those of typical *guttata* in both herbarium and cultivated material, and are only loosely correlated. The more compact Welsh and Irish plants appear to be comparable with plants in similar exposed coastal habitats in north-west France. It is concluded that *T. guttata* shows ecotypic differentiation in relation to exposure on the Atlantic coast of Europe, and that the populations combining short diffuse habit and numerous bracts may be of polytopic origin. It is suggested that they should not be given formal taxonomic recognition.

1. INTRODUCTION

Like a number of other widespread Mediterranean species, *Tuberaria guttata* extends northwards up the west coast of Europe to a northern limit in the British Isles. Up to the north coast of France its distribution is more or less continuous, and the Channel Islands lie on the northern fringe of this essentially continuous area. But north of the English Channel its range is disjunct, and it occurs only in widely separated colonies on the coasts of north Wales and western Ireland. Plants from the best known of these colonies, on Holyhead Mountain in Anglesey, were described by Planchon in 1844 as a new species, *Helianthemum breweri*, and, as a variety or subspecies, *breweri* has become firmly established in the British literature. Authors have differed considerably in the value they have attached to the various characters said to separate it from typical *T. guttata*, and in the British populations that they have referred to *breweri* and to *guttata*. Most seem to have assumed that it was deserving of taxonomic recognition, and that all British plants could be assigned satisfactorily either to *breweri* or to *guttata*. The purpose of this paper is to show that none of the delimitations of *breweri* proposed hitherto is completely satisfactory, and that the variation pattern in *T. guttata* in Britain and neighbouring parts of the Continent is more complicated, and taxonomically intractable, than has usually been assumed.

2. THE HISTORY OF *HELIANTHEMUM BREWERI* PLANCH.

The Holyhead colony of *Tuberaria guttata* was discovered by Samuel Brewer in 1726 (see Hyde 1930). Dillenius wrote to Brewer on 31 May 1727 'I desire him (i.e. the Rev. Mr. Green) to look after the plant you sent from Holyhead . . . It is a *Cistus* and seems to be new.' Brewer received further specimens of the plant from Mr. Green on 5 August 1727. Dillenius had evidently intended to describe the plant himself, but, in the event, it was first mentioned in print over half a century later by Hudson (1778), as '*Cistus guttatus* . . . Habitat in pratis arenosis, in monte Llech ddû prope Holyhead in insula Mona.' Curtis (1775-98) figured under the same name a bracteate and spotted-petalled plant, but did not say whether it was wild or cultivated, and gave the Isle of Man as a locality, evidently mistranslating 'Insula Mona.' In this he was followed by Sowerby & Smith (1790-1814, t. 544), who figure a rather stiffly formal little plant with numerous bracts and say that 'Having no hopes of obtaining wild specimens in a state fit for drawing, we have been

obliged, like Mr. Curtis, to have recourse to a garden one, communicated by the Rev. Mr. Watts, F.L.S. of Ashill, Norfolk . . . ' Smith (1800) gave the localities ' In Jersey, Sherard. In the Isle of Man, Mr. Brewer. Huds.' and his description notes ' . . . saepius ebracteati, interdum bracteis lanceolatis, solitariis, ad basim pedicellorum.' Later (1825), quoting the Rev. H. Davies, he correctly gave the locality as Anglesey. Supposedly Manx plants were distributed by Dickson (*Hortus Siccus Britannicus*), 1793-9, but the specimens are tall slender plants quite unlike any other British examples of *T. guttata*. As far as I know, there is no other evidence that they actually came from the Isle of Man, and they are probably garden specimens to which the name of the (supposed) best-known British locality was attached.

Planchon knew *T. guttata* well in the south of France, and saw specimens of the Holyhead plant in the herbarium of W. Wilson of Warrington. He says (Planchon 1844) ' the straggling mode of growth, with short, numerous and dichotomous bunches of flowers, the existence of bracteas even to the upper flowers, and of pedicels, which at first bend down, but rise up when the fruit is ripe and stand at an angle of forty-five degrees to the axis of the cluster, such were the characters, which at first glance, suggested the idea that the plant was specifically distinct from *H. guttatum*.' Planchon knew that cultivation made no difference to ' the main point,' the presence of bracts. He gives a terse diagnosis, followed by a longer Latin description:

HELIANTHEMUM BREWERI, Planchon

Helianthemum (e sectione *Tuberaria*); annum a basi ramosum subdiffusum viscidulo-hispidulum, pedicellis bracteatis, defloratis subdeflexis, fructiferis erecto-patentibus, petalis angustis immaculatis, staminibus 8-12, seminibus quam in *H. guttato* majoribus.

Cistus guttatus, *Huds. Fl. Angl.*, p. 232, *ex local. citat.*

Cistus guttatus, *Smith Fl. Brit. t. 2, p. 573*, (*pro parte et quoad plant. Brewerian, non Engl. Bot.*).

HAВ. Anglesey, Mr. Brewer, (Hudson), Holyhead Mountain, *Rev. Mr. Williams*, and also near Amlwch, *Rev. H. Davies, W. Wilson, Esq.*

Herba a basi ramosa, vel, axi abbreviato pluricaulis, viscidulo-hispida. Caules 4-6, subdiffusi, semel bis-trichotomi, in racemos laxos, bracteatos desinuentes. Folia pauca, opposita, sessilia, inferiora 4-6, rosulata, late obovata, semipollicaria, obtusissima; caulina stipulata, lineari oblonga, obtusiuscula, omnia pilis stellatis simplicibus intermixtis, utrinque hispidula. Bracteae conspicuae, lineares, non raro falcatae, inferiores 3-4 lin. longae, hinc ad summos flores gradatim minores, nunquam deficientes. Pedicelli graciles, 6-8 lin. longi, floriferi subdeflexi, deflorati diu sic persistentes, tandem, maturo semine, erecto-patentes. Calyx ut in *H. guttato*. Sepala conspicue nigropunctata; trium majorum alterum latus in praefloratione tectum, petaloidea-membranaceum. Petala in flore unico observata, angusta, lutea, immaculata. Stamina definita (8-12) pistillo vix longiora. Ovarium et fructus vix *H. guttati*, sed semina pauciora et evidenter majora.

Planchon emphasised the short diffuse habit of growth and the presence of bracts as the most important characters of his new species. He had seen an imperfect specimen of the Jersey plant, and considered it ' merely a hispid variety of *H. guttatum*.'

The *Annals and Magazine of Natural History* for the same year contains an account of a meeting of the Botanical Society of London, at which W. R. Crotch exhibited specimens of Planchon's new species, and a note by C. C. B[abington] reporting ' true *H. guttatum*,' collected at Three Castles Head by Miss H. Townsend.

H. breweri appeared in the second edition of Babington's *Manual of British Botany* (1847) as a separate species, the presence of bracts being given as a diagnostic character. Bentham (1858) says rather non-committally ' . . . the Anglesea specimens are rather stunted, with the leaves broader than usual, and have been published as a species under the name of *H. Breweri*.' Hooker and Arnott (1860) give *breweri* as a variety under *H. guttatum*. In the seventh edition of the *Manual* (1874), Babington reduced *breweri* to a variety of *guttatum*, and altered the description to ' Racemes with or without bracts on the same plant.' Syme (1864) and Hooker (1870) rank the plant as a subspecies of *H. guttatum*. Inishbofin, W. Galway, was added to the list of localities of var. *breweri*

by A. G. More (1876), and appeared in the ninth edition of Babington's *Manual* (1884); according to Praeger (1901) 'The var. *Breweri* accompanies the type at Three Castles Head and Inishbofin, and alone grows on Inishark.' (see below for detailed list of localities).

Planchon's conclusions seem to have been generally accepted by British botanists, who contrasted *breweri* with the Channel Islands plant: indeed tall ebracteate plants from the *locus classicus* of *breweri* were named *guttata* by J. G. Baker (Druce 1890, 1891). But Griffith (1895) says 'I have sown seeds of the supposed *H. guttatum* and seeds of undoubted *H. Breweri* from the same place in rich soil in my garden, with the result that they all turned out to be the same - viz. *H. Breweri*.' In this conclusion he is strongly supported by Druce (1902) who considered that '... the characters given to *H. breweri* both by its original describer and subsequent writers will need amending; as those of bracteate inflorescence, diffuse growth, and unspotted petals given by Planchon are found to be inconstant... Still, the Anglesey plant has a different facies from the *H. guttatum* of Jersey, the leaves being broader and more obovate, and of a more coriaceous texture... and I think it to be a good geographical race.' Druce had earlier (1893) named the ebracteate plants from Holyhead 'f. *ebracteata*.'

Grosser (1903), regarding *T. guttata* on a continental scale, united populations on the west coast of Europe from Wales and Ireland to Portugal in var. *breweri*. The main diagnostic characters of his variety are low, diffuse habit, and the pubescence of the leaves, which are described as hispid and densely stellate-tomentose on both surfaces: he makes no mention of bracts. The distribution of the variety is given as 'Strandgebiete von West-England und Nord-West-Frankreich entlang der westfranzösischen Küste bis in das maritime Nord- und Mittel-Portugal (Sierra de Cintra).' He cites *Welwitsch It. Lusit.* (1840) nos. 433, 1317, 1526 and (1851) no. 49, and includes *H. guttatum* var. *maritimum* Lloyd and *H. litorale* Rouy and Fouc. as synonyms. As he included England among the localities for his var. *genuina*, it seems that he accepted the opinion of British botanists that at least the Channel Islands material belonged to typical *T. guttata*.

Warburg (1952) accepts Grosser's statement of the Continental distribution of *T. guttata* var. *breweri*, and his description and account of its British distribution follow accepted British opinion. In my account of *T. guttata* for the *Biological Flora* (Proctor 1960), I suggested that the name *breweri* should be limited to the Welsh and Irish populations; though recognising that the taxon so defined was not completely satisfactory. At my suggestion, Dr. Warburg adopted this delimitation of subsp. *breweri* in the second edition of the *Flora* (1962).

3. THE VARIATION IN BRITISH *T. GUTTATA*

(a) *Distribution*

I believe the following list of the British localities of *T. guttata* is substantially complete: I have cited specimens and literature records only in the case of less well-known localities, or where the record is otherwise interesting.

- V.c. S. CHANNEL ISLANDS. Jersey: West Mount, St. Helier; Noirmont; St. Brelade's Bay; Beauport; La Moye; Portelet; Corbière; Petit Port; headland north of Petit Port; L'Etac (Lester-Garland 1903); above Pinnacle Rock, between L'Etacq and Grosnez (F. Le Sueur, March 1960); 'observed in Jersey by Mr. Sherard on the west-side of the Island near Grosnez Castle.' (Ray 1690 p. 238); Grosnez (Lester-Garland 1903). Alderney: south coast, on cliff top west of Val du Sud. (Except where specific references are given, specimens from all localities are in either K, BM or CGE).
49. CAERNS. Mainland opposite Bardsey I. (1938, W. Hughes D'Aeth), 1939 (and det.) Miss B. M. Morgan (*Rept. Bot. Soc. Exch. Cl.* for 1943-4, 705 (1946)).
52. ANGLESEY. Holyhead Mountain, S. Brewer, 1726, and many more recent collectors; near Porthdafarch, C. C. Townsend, 8 July 1952 (herb. Townsend); 'Lady Verney tells me she has found this [*H. breweri*] in another locality about three miles from the *locus classicus* in Anglesey.' (Druce 1919) (Perhaps the same locality as the last); between Clegyr Mawr and the

- sea, Llanrhyddlad (Griffith 1895, as *H. breweri*); Gader [Trwyn y Gader = Carmel Head] in the parish of Llanvair in Cornwey [Llanfairynghornwy] at the north end of the Island facing the Skerries about half a mile from the sea upon the rocks where the soil is not deep, among the *Scilla bifolia* and *Sedum rubens*: it flowers in June. Mr. Williams [undated] (BM); Amlwch, i.e. N.W. of the Village among Heath, before the discovery of the great copper mine, plentifully, H. Davies [undated] (BM).
- H3. W. CORK. Three Castles Head (Babington, 1844; Moore & More, 1866, as *H. guttatum*); *ibid.*, type and var. *breweri* (Colgan & Scully 1898; Praeger 1901); Calf Islands (Praeger 1934).
- H16. W. GALWAY. Inishbofin (type and var. *breweri*), Inishark (var. *breweri*) (Colgan & Scully 1898; Praeger 1901).
- H27. W. MAYO. Inishturk (Praeger 1934).

(b) *Cultivation experiments*

My own cultivation experiments were begun in 1953, the most extensive being carried out in 1956, 1959 and 1961 (see Figs. 3-6). It was found most convenient to grow plants singly in four-inch pots (1956) or in rows in boxes (1959, 1961). The seeds are hard-coated, and it often proved difficult to germinate enough seeds from all the populations at nearly enough the same time for the seedlings to be comparable. Plants grown from wild-collected seedlings were several weeks more forward than those grown from seed germinated in the garden, and all plants took much longer to flower and fruit than in the wild. Indeed in Cambridge it was often difficult to induce the Three Castles Head plants to flower at all.

T. guttata is a plastic species, and the different conditions of different years produced very different-looking plants, so that comparisons cannot be made between populations grown in different seasons. However, the relative differences between populations in any one season were not greatly affected. From comparison of several years' results I am satisfied that the main conclusions set out below are generally true, though further experiments would quite probably produce results differing in detail from mine. In spite of some difference in the age of the seedlings, plants from any one population were generally rather uniform in size and other characters, and I found no evidence for the coexistence of two taxa in any British population.

In a number of cases seed was saved from cultivated plants for later experiments. This was made easier by the fact that the plants grown were apparently all normally self-pollinated: as additional precautions, plants kept for saving seed were isolated as far as possible, or seed was used which had set when other populations were not in flower.

(c) *General observations on the taxonomic characters*

Of the characters emphasised by Planchon, the 'narrow unspotted petals' were based on observation of only a single, aberrant, flower. Seed size has received little attention. Seed lengths for a number of samples of *T. guttata* are given in Table 1. There is an evident tendency for the northern and western populations to have somewhat larger seeds, but there is too much local variation, both in north and south Europe, for this to be a useful diagnostic character.

The presence of bracts was recognised to be inconstant by Babington and Druce, and the size and number of bracts produced depends at least in part on environmental conditions. Thus on the one hand it is possible to find ebracteate individuals in populations of generally bracteate '*breweri*,' while on the other hand plants of *T. guttata* from Jersey grown in Exeter produced numerous bracts. The bracts are of two kinds. Broad leafy bracts are sometimes seen in the lower part of the inflorescence, and it is not always easy to differentiate between these and the uppermost leaves. Higher up the inflorescence the bracts resemble the narrow outer sepals in shape and texture. These small bracts may become almost constant in the upper parts of inflorescences which are wholly ebracteate below (e.g. from about the fifth flower in La Moye plants, and the third in Holyhead

TABLE 1.
Seed length in some populations of *Tuberaria guttata*.

<i>Provenance</i>	<i>Number of seeds measured</i>	<i>Mean length (mm)</i>	<i>Standard deviation</i>
Messina, Sicily	5	·584	·042
Monte Nuovo, Naples	6	·534	·045
Appenines between Florence and Bologna	5	·699	·066
Sintra (Estação Agronómica Nacional)*	10	·559	·044
Sintra (I. A. Williams)*	10	·688	·060
Welwitsch It. Lusit. 433	5	·501	·037
Toulon	5	·613	·054
Montpellier	4	·613	·046
Lyon, à la Pape	5	·598	·042
Mouilleron-en-Pareds, Vendée	5	·662	·053
Croisic, Loire-inf.	5	·560	·035
Baie des Trépassés, Finistère*	10	·636	·030
Corbière, Jersey*	10	·621	·038
L'Etacq, Jersey*	10	·608	·041
Ffynnon Fair, Caerns.*	10	·739	·070
Holyhead, Anglesey*	10	·702	·073
Clegyr Mawr, Anglesey*	10	·675	·048
Inishbofin (Middle Quarter)*	10	·703	·045

For further details of populations marked with an asterisk, see appendix. The other measurements are from herbarium specimens in CGE.

TABLE 2.
Measurements of herbarium specimens of British *T. guttata*. This table is based mainly on material in BM, with some Welsh and Irish material from CGE, EXR, K and herb. C. C. Townsend.

<i>Provenance</i>	<i>Specimens examined*</i>	<i>Height (cm)</i>		<i>% diffuse habit</i>	<i>% pedicels with bracts</i>	<i>% with stellate pubescence on upper leaf surface</i>
		<i>mean</i>	<i>s.d.</i>			
Channel Isles						
Jersey (S. Coast)	21	10·47	4·64	50	9	100
Jersey (W. Coast)	49	9·49	3·57	35	3	96
Alderney	2	15·0	—	0	0	100
Wales						
Opposite Bardsey Island	5	3·2	0·75	0	—	100
Holyhead	59	3·49	1·96	21	60	94
Porthdafarch	9	10·22	2·35	0	62	89
'Gader'	12	5·17	2·33	8	21	100
Clegyr Mawr	5	7·2	2·49	0	20	100
Ireland						
Three Castles Head	13	6·08	2·04	31	19	23
Inishbofin	14	5·86	1·72	24	29	79

*These are the numbers of specimens whose height was measured: in several cases it was not possible to score all of these for bract number and stellate pubescence. Several of the small sets of data are based on one or a few gatherings, and in these cases the figures given are not suitable for a significance test of the difference in height between populations, since season-to-season differences contribute variation which may not be adequately reflected in the standard deviations.

plants, among material cultivated in 1961), so there is a general tendency for the proportion of bracts to flowers to rise as the season advances (see Table 3). There is a negative correlation, but not a close one, between plant height and bract number ($r = -0.24$ in cultivated material in September 1961 (not statistically significant, $P > 0.3$): if the La Moye plants are ignored as possibly aberrant, $r = -0.75$; $P \approx 0.05$).

TABLE 3.

Height and bract frequency of plants of *T. guttata* cultivated in 1961. The upper measurement in each row was made on 8 Aug. 1961, the lower on 8 Sept. 1961.

Population	Number of plants measured	Height (cm)		% pedicels with bracts
		mean	s.d.	
Brittany				
Baie des Trépassés	4	7.5	2.0	0
	3	12.3	0.47	0
Channel Islands				
La Moye	2	15.0	1.0	23
	2	16.5	1.5	47
Corbière	9	10.6	2.27	7
	8	13.1	0.93	13
L'Etacq	9	4.1	1.37	—
	8	10.6	0.70	36
Wales				
Holyhead	6	3.8	0.69	—
	2	9.0	1.0	63
Clegyr Mawr	8	5.9	3.1	0
	7	9.7	1.7	13
(Clegyr Mawr*)	7	14.9	0.84	19
Ffynnon Fair	6	5.2	0.69	—
	5	10.0	1.6	32
Ireland				
Inishbofin	10	3.0	—	—
	6	6.3	0.94	53

Druce considered relative leaf-width a more useful and more constant character of Holyhead *breweri* than any of the foregoing. However, if the logarithm of leaf-width is plotted against the logarithm of leaf-length, the points for all populations fall near to a straight line. This suggests that the relation of leaf-breadth to leaf-length is allometric, and that the essential difference between the '*breweri*' populations and typical *guttata* is the obvious one of size. Environmental factors evidently affect the relation between leaf-breadth and -length, and the leaves of plants in cultivation are regularly wider than those of plants in wild habitats.

There remain the characters of stature and habit. The size of the plant depends greatly on environment, so that although stature differences may be striking in the field, cultivation experiments are necessary to assess their significance. In cultivation, different

*Wild-collected seedlings, measured 8 Aug. 1961.

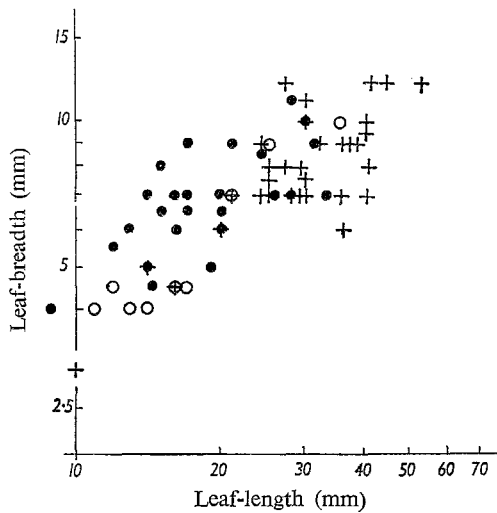


Fig. 1. Log leaf-breadth plotted against log leaf-length for lower cauline leaves of 68 herbarium specimens of *T. guttata*. Crosses, Channel Isles material; solid dots, Wales; open circles, Ireland.

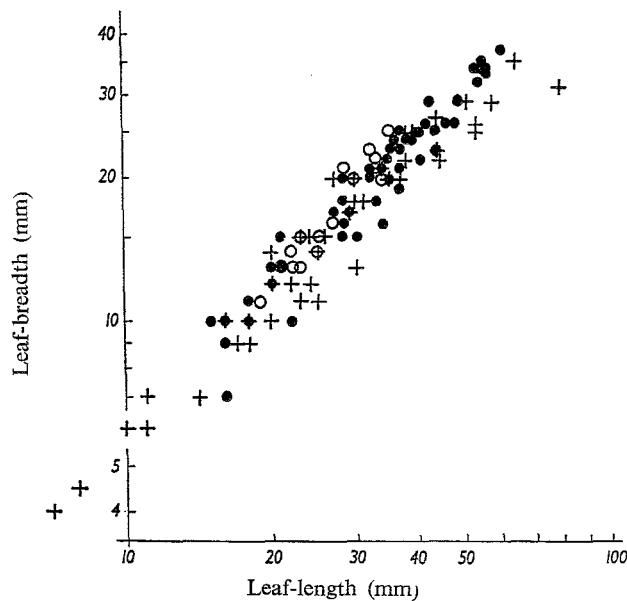


Fig. 2. Log leaf-breadth plotted against log leaf-length for basal rosettes of *T. guttata* in cultivation. The graph is based on two measurements, taken on 8 and 20 June 1961, of the longest rosette-leaf of each of 62 plants. The measurements are taken from the same material as Figs. 5 and 6. Symbols as in Fig. 1.

populations matured at different rates, southern plants in general developing more rapidly and flowering earlier than those from further north. Hence it was possible for plants to be similar in size and habit in the rosette stage and at maturity, but strikingly different at any one moment in the intervening period (see figs. 3-5). These differences in rate of maturation are obviously important taxonomically and physiologically: so far as possible I have avoided their incidental effects on other characters by making comparative

measurements on mature plants. Diffuse habit of growth is not as useful a character as it appears at first sight. Simple individuals can be found in all populations of *T. guttata*, especially in dry seasons. All the populations I have grown become more diffuse in cultivation, and, given sufficient water, more diffuse as the season progresses, and the differences observed in the field are probably very largely a direct reflection of habitat conditions, especially water-supply and competition. The inflorescence does not appear to me to provide any clear characters apart from length which might separate *breweri* from typical *guttata*: the pedicels in all the British populations appear to behave in the same way as Planchon describes for *H. breweri*.

It is interesting, as Druce (1919) points out, that cultivation tends to accentuate several of the features usually considered characteristic of *breweri*; diffuse habit, broad leaves, and the occurrence of bracts. Without cultivated plants of typical *T. guttata* for comparison this undoubtedly presented Planchon and Griffith with an even more striking picture of the difference between Holyhead *breweri* and Channel Islands *T. guttata* than that which really exists.

(d) *Comparison of British populations*

The Channel Islands plants do not differ in any taxonomically significant way from the plants of neighbouring parts of the French coast, and they are the standard by which other populations have generally been judged by British botanists. Tall sparingly branched plants from Jersey can be matched closely in habit, leaf shape, and inflorescence with plants from as far afield as Spain and Calabria; but taken as a whole the Channel Islands plants are shorter and more branched than south European populations. Typically they range from about 5–15 cm in height, with 3 or 4 pairs of opposite cauline leaves above the basal rosette. Even vigorous individuals are often sparingly branched; but plants showing diffuse branching from the base are also common. The leaves are pilose or hispid on both surfaces, and stellate-hairy below; and almost invariably show a greater or lesser amount of stellate tomentum above. They are usually said to be ebracteate, but bracts occasionally occur in wild plants, often several on one individual (see Table 2). Their scarcity in wild material probably reflects the fact that flowering is over much earlier in Jersey than in the more northern and western localities. There are usually one or more alternate, lanceolate, stipulate leaves between the opposite-decussate lower cauline leaves and the first flowers. In cultivation, plants from Jersey show substantial variation in size and in the number of bracts produced.

Plants from the *locus classicus* of *breweri* at Holyhead are shorter (usually less than 10 cm), and vigorous examples are normally diffusely branched. However, small impoverished plants are usually simple, and in fact diffuse branching was found to be substantially less frequent in herbarium material from Holyhead than in that from the Channel Islands. There are most commonly 3 pairs of opposite-decussate cauline leaves, and the alternate, stipulate, upper cauline leaves are often absent. As Druce observes, the leaves are dark green, rather coriaceous in texture, and relatively wider than those of Jersey plants (but see pp. 241–2). Stellate hairs are usually present on the upper surface of the leaf, forming a sparse felt, at least near the apex. Bracts are usually present, subtending some or all of the pedicels, but by no means constantly so. The Holyhead plants have a rather distinctive appearance, with their short rigid spreading inflorescences, and their compact dark green vegetative growth. They remain shorter than the Channel Islands plants in cultivation. Their habitat, in the bare patches between wind-cut heathers on the steep slopes above the cliffs facing South Stack, is extremely exposed.

The Caernarvonshire locality opposite Bardsey Island is equally exposed: specimens I have seen from here are similar in stature to Holyhead plants (2–4 cm), but simple and more slender in habit. In cultivation they differ in their untidier and more vigorous vegetative growth, fewer bracts, and in the less coriaceous texture and paler colour of the leaves: they become almost as tall as the most compact of the Jersey plants (l'Étacq).

Plants from the Clegyr Mawr colony are similar in stature, but with laxer inflorescences (mean distance between successive pedicels in 1961 experiment 8.66 mm, against 7.20 mm in material from Ffynnon Fair; difference significant at $P < 0.05$), and the presence of bracts is much less constant. Some herbarium specimens can scarcely be distinguished from the largest plants collected at Holyhead, while others do not differ in any significant respect from small Channel Islands plants, which plants from this population resemble in cultivation. The Clegyr Mawr population grows among low wind-cut heather on a slight rocky knoll in the shallow valley leading from Clegyr Mawr to the sea, and is probably considerably less exposed than either the Holyhead or Lleyrn populations. The exact location of Williams's population 'Gader . . . facing the Skerries . . . ' is not certain. His specimens resemble the Clegyr Mawr plants, and it is perhaps possible that the locality is the same. His description suggests a position near Carmel Head (*c.* Nat. Grid Ref. SH 296924), where there is certainly suitable-looking ground, but if *T. guttata* occurred here I have been unable to re-find it. In any case the habitat must have been less exposed than at Holyhead.

Irish plants from Three Castles Head, Inishbofin, and Inishturk are all diffuse in habit when well-grown, though they are extremely plastic and, as in Wales, starved specimens are often simple. Bracts are often present, though less regularly than in the Holyhead plants: they appear to be significantly more frequent on Inishbofin than at Three Castles Head. I have not seen herbarium material from the Calf Islands, but there seems to be little variation in size and habit in Irish *T. guttata* from the remaining localities beyond that due to plasticity (though there is a surprisingly tall, simple, specimen from Three



Fig. 3. 1956 cultivation experiment; silhouettes of representative plants, $\times \frac{1}{4}$. a, Jersey; b, Baie des Trépassés; c, Clegyr Mawr, Anglesey; d, Holyhead, Anglesey; e, Three Castles Head, Co. Cork.

Castles Head in Babington's herbarium (CGE)). Plants grown from seed from Three Castles Head and Inishbofin uniformly produced very dense much-branched leafy rosettes, with many short inflorescences late in the summer.

TABLE 4.

Ranking of cultivated material of six populations of *T. guttata* by seven characters (1961 experiment).

Population	Height (tall- short)	Bract frequency (few- many)	Leaf colour (dark- light)	Stem pubescence (sparse- dense)	Number of branches (many- few)	Order of flowering (early- late)	Seed length (small- large)
Corbière	1	1	1	1	2	1	2
L'Etacq	2	4	2	5	6	3	1
Ffynnon Fair	3	3	6	6	4	6	6
Clegir Mawr	4	2	4	3	5	4	3
Holyhead	5	6	3	2	1	2	4
Inishbofin	6	5	5	4	3	5	5

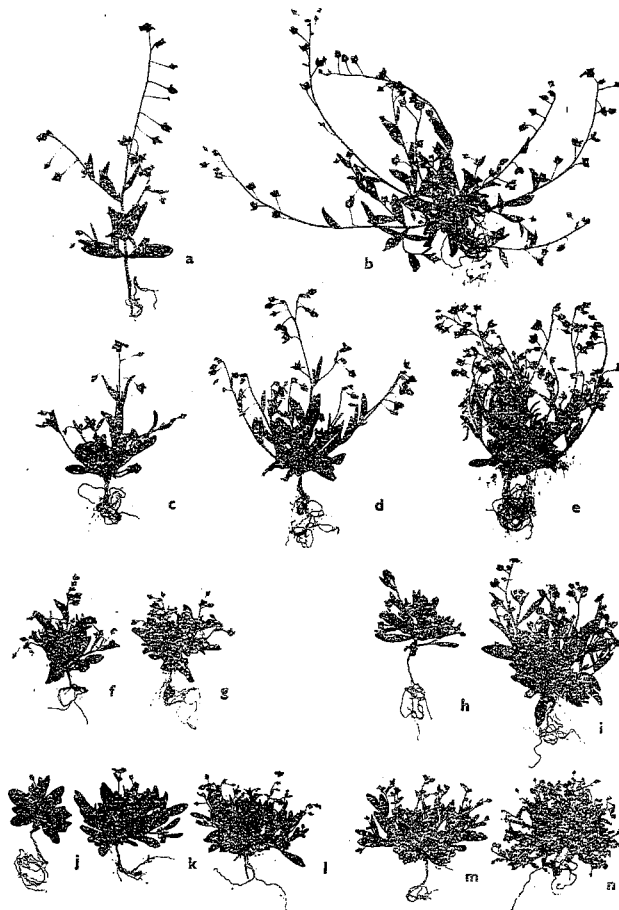


Fig. 4. 1959 cultivation experiment; silhouettes of representative plants, $\times \frac{1}{2}$. a, Sintra, Portugal, 20 July; b, *ibid.*, 27 Aug.; c, Jersey, 20 July; d, *ibid.*, 28 July; e, *ibid.*, 4 Aug.; f, Holyhead, 20 July; g, *ibid.*, 4 Aug.; h, Ffynnon Fair, 28 July; i, *ibid.*, 27 Aug.; j, Middle Quarter Hill, Inishbofin, 28 July; k, *ibid.*, 18 Aug.; l, *ibid.*, 27 Aug.; m, West end of Inishbofin, 18 Aug.; n, *ibid.*, 27 Aug.; The dates given are when plants were pressed.

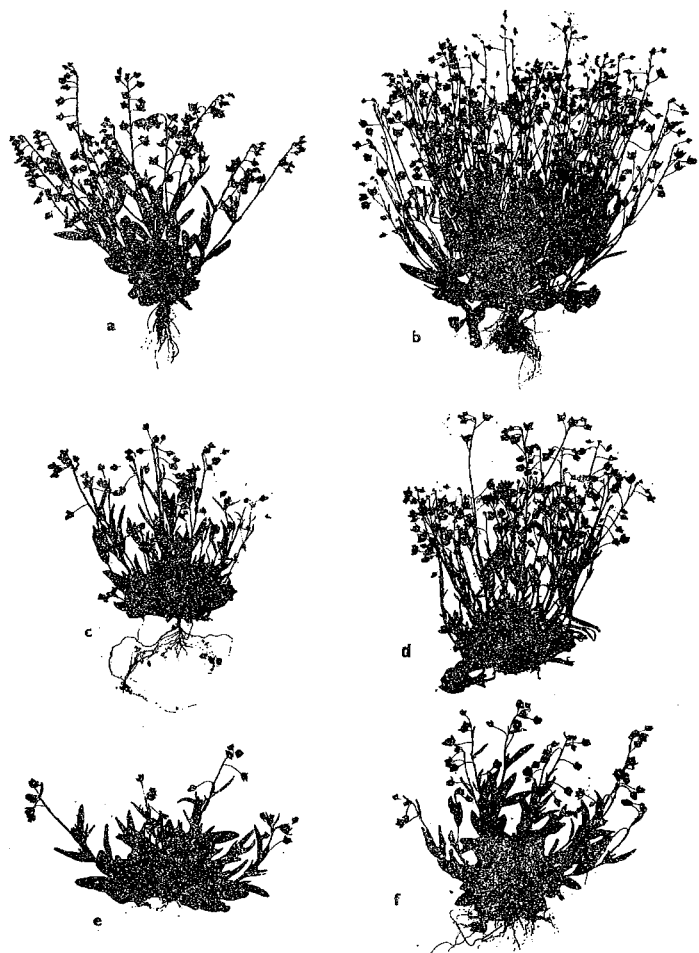


Fig. 5. 1961 cultivation experiment: material from Brittany and the Channel Islands, $\times \frac{1}{4}$. a, Baie des Trépassés, Brittany, 8 Sept.; b, La Moye, Jersey, 8 Aug.; c, Corbière, Jersey, 8 Aug.; d, *ibid.*, 8 Sept.; e, L'Etacq, Jersey, 8 Aug.; f, *ibid.*, 8 Sept.

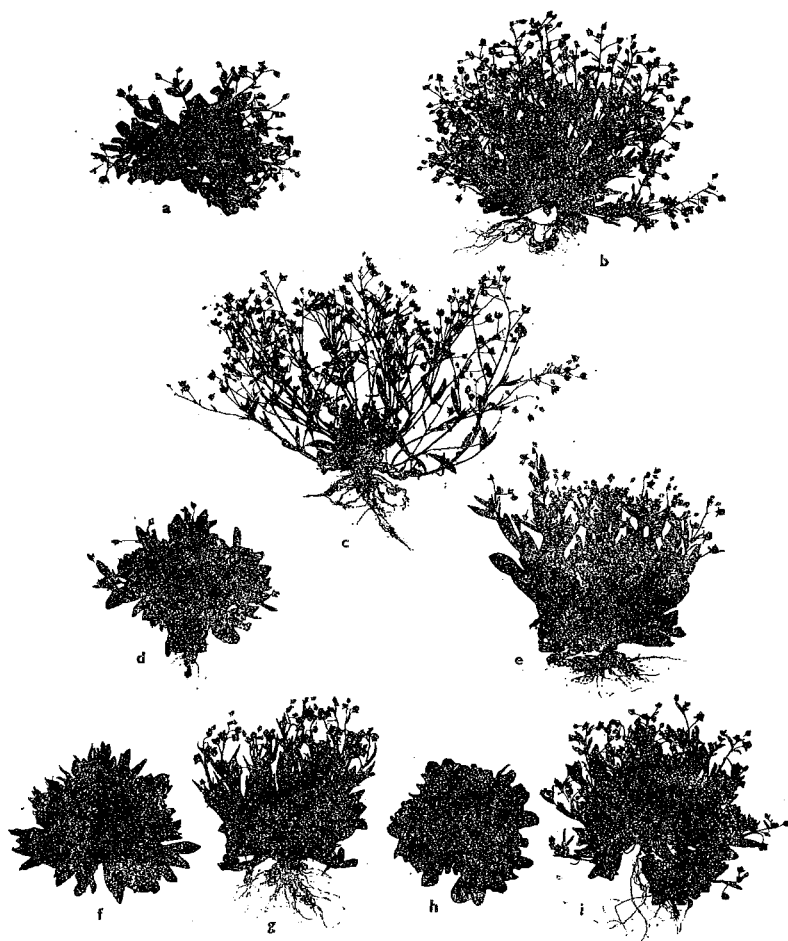


Fig. 6. 1961 cultivation experiment: material from Wales and Ireland, $\times \frac{1}{4}$. a, Holyhead, 8 Aug.; b, *ibid.*, 8 Sept.; c, Clegyr Mawr, 8 Aug. (from wild-collected seedlings); d, Clegyr Mawr, 8 Aug.; e, *ibid.*, 8 Sept.; f, Ffynnon Fair, 8 Aug.; g, *ibid.*, 8 Sept.; h, Middle Quarter, Inishbofin, 8 Aug.; i, *ibid.*, 8 Sept.

TABLE 5.

Spearman rank correlation coefficients calculated from the data of Table 4. Only in the cases of the correlations between flowering date and leaf colour and stem pubescence, and between seed length and leaf colour is ρ great enough to establish a significant correlation between two characters with $P < .05$. However, in all the remaining cases the departure from unity demonstrates the absence of close correlation.

	<i>Bracts</i>	<i>Colour</i>	<i>Pubescence</i>	<i>Branching</i>	<i>Flowering date</i>	<i>Seed length</i>
<i>Height</i>	.71	.60	.09	-.24	.43	.60
<i>Bracts</i>		.26	.20	-.24	.15	.31
<i>Colour</i>			.66	.14	.94	.89
<i>Pubescence</i>				.66	.83	.37
<i>Branching</i>					.43	-.37
<i>Flowering date</i>						.71

In size and habit the populations form a graded series from the tallest plants from Jersey (La Moye) to the most compact Irish plants from Inishbofin. The relation between height and some other characters is illustrated in Tables 4 and 5. Of these characters, only bract number and leaf colour are markedly correlated with height, and even here the correlation is not statistically significant at the 5% level. In general, each character is correlated with not more than four others: two characters (e.g. bract frequency and leaf colour) may both show correlation with a third character (e.g. height), without themselves being closely correlated. The whole body of data suggests a network of loose correlations in several unrelated directions, in which no single direction of variation predominates strongly over the others. It is noteworthy that in Table 5 the variation associated with leaf colour and flowering date appears to be at least as important as that associated with the more familiar and obvious characters of height, and frequency of bracts.

(e) *T. guttata* in north-west France

Plants on the exposed coasts of Brittany and the Bay of Biscay are characteristically short in stature and diffuse in habit, usually with rather denser stellate and simple pubescence on the upper surface of the leaves than in the British populations. Some (including the only sample I have had in cultivation) closely resemble the Channel Islands plants and are more or less ebracteate; but populations exist which appear to be very comparable with the populations at Holyhead and in the west of Ireland: low-growing much-branched plants, with short bracteate inflorescences, e.g. Rochers mar. de Pornichet à Chemaulin (Loire-inf.), July 1874, Herb. E. Gadeceau (BM); St. Brevin (Loire-inf.), 23 June 1856, J. Lloyd (BM); Croisic (Loire-inf.), 23 June 1880 J. Lloyd (BM); *ibid.*, June 1851, Drs. Thuret & Broceaux [?], Herb. Gaston Genevier (CGE). These variable west coast plants were described by Lloyd (1876) as *H. guttatum* var. *maritimum*.

maritimum. *H. alyssoides* Pesn. cat., 59, non Vent. Plante de 5-10 cent. rameuse, étalée, hérissée, blanchâtre; rac. épaisse, dure, mais [annuelle]. Rochers marit.

Rouy & Foucaud (1895) call the plant *Helianthemum litorale*, citing Lloyd's name as a synonym, and they give stature and presence of stellate pubescence on the upper surface of the leaves as diagnostic characters. The habitat is given as "Rochers maritimes des bords de la Manche et de l'Océan." Neither Lloyd nor Rouy & Foucaud mention bracts. The specimens mentioned above, collected by Lloyd and named var. *maritimum*, are bracteate, but the name evidently included taller and more or less ebracteate plants

as well, e.g. Falaise de Carteret, (Manche), 31 May 1888, Herb. L. Corbière (K), which is very like material from the more exposed localities in Jersey. What is particularly significant is Lloyd's comment after his description of var. *maritimum*: 'Revient graduellement au type, à mesure que l'on s'éloigne de la mer.'

It appears, then, that in north-west France we have the common pattern of a widespread species passing gradually into a dwarf maritime ecotype on exposed rocky cliffs; a correlation between the 'breweri' characters and exposure is also apparent in Britain, and it seems reasonable to suppose that the disjunct British populations represent scattered fragments of a similar pattern. A similar pattern may also exist on exposed coasts in N. Spain and Portugal: the plants cited by Grosser provide little evidence of it, but two very short compact flowering specimens (c. 1.5–2 cm high) in the Kew Herbarium (Adjuda Hill, Lisbon, May 1935, *S. C. Atchley* Fl. Portugal 401; Foothills facing the Atlantic between Estoril and Cintra, May 1935, *S. C. Atchley*, Fl. Portugal 402), look much more likely to be comparable with British 'breweri.' They differ from any British or French material in their very dense grey stellate tomentum with only sparse simple bristles. The common feature running through the extreme west coast forms of *T. guttata* is the short much-branched growth habit, often associated with bracteate inflorescences: in fact the characters emphasised by Planchon as distinguishing *breweri*. This may be due to a tendency for other, non-adaptive, characters to show developmental correlations with the characters responding to selection for short stature, and perhaps for long vegetative period; and if this is so, the 'breweri' characters are likely to be of polytopic origin in the various populations. The differing indumentum of British and French (and Portuguese) plants, and the variation in frequency of bracts and other characters in the British populations, are consistent with this possibility. It would be interesting to know something of the morphogenesis of the leaf and shoot pattern in *T. guttata*.

4. DISCUSSION

The question arises whether these diverse populations can be distributed into useful taxa. The two extreme, and simple, possibilities are either to limit the name *breweri* to the Holyhead population, or to follow Grosser and adopt a wide delimitation of *breweri* to include a range of Atlantic coast plants, of varying stature, with or without bracts. The first possibility would logically require similar separate taxonomic recognition of the Caernarvonshire, Irish and north-west French *breweri*-like forms, and although there are zoological precedents for a treatment of this kind in dealing with isolated small populations within the British Isles, I feel that this would be of little scientific value in the case of a generally variable species like *T. guttata*. On the other hand, Grosser's delimitation of *T. guttata* var. *breweri* provides no satisfactory line of distinction from typical *guttata*. Stellate pubescence on the upper surface of the leaves is commoner near the Atlantic coast, but it is found in a proportion of plants throughout much of the range of the species (and in the British Isles it is least constant at Three Castles Head!). Grosser's delimitation results in the abandonment of virtually all the characters of Planchon's original *H. breweri*. Willkomm's figure of *T. variabilis* var. *cinerea* ('ad specimen Welwitschianum delineatam') is certainly rather like the Welsh and Irish plants, and has a few bracts; but specimens at Kew and Cambridge show *Welwitsch It. Lusit.* (1840) No. 433 (which Willkomm and Grosser cite) to be a rather tall plant (11–23 cm), having little in common with the Holyhead plant. The Channel Islands plants can scarcely be excluded from Grosser's variety, though by implication he seems to include them in typical *guttata*; and they were specifically excluded from the original delimitation of *breweri* and included in typical *guttata* by Planchon.

Any intermediate treatment breaks down over one or both of two difficulties: the difficulty of providing usable and taxonomically meaningful lines of demarcation, and the fact that most of the possible groupings of the populations obviously lack genetic coherence. The extreme populations are certainly strikingly different from typical *T. guttata*, but on

analysis their characters reduce to the slight, and obviously adaptive, one of stature, in which they intergrade with the typical form of the species. Other characters, which might be expected to be taxonomically more reliable, do not correlate at all closely with this, and do not appear to show any major taxonomically significant pattern of their own.

There is a strong argument for simply recognising the existence of a pattern of ecotypic differentiation in north-west European *T. guttata* in relation to exposure, and not attempting any formal taxonomic treatment of it. On the present evidence I am forced to the conclusion that no orthodox taxonomic treatment of the variation in these *T. guttata* populations is practicable or of any real value.

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APPENDIX : MATERIAL OF *T. GUTTATA* USED IN CULTIVATION EXPERIMENTS

- Jersey. Seed from cultivated plants, probably originally from near Corbière. D. McClintock.
Near Corbière, Jersey, 22 March 1960, Mrs. F. Le Sueur.
Above Pinnacle Rock, between L'Etacq and Grosnez (on granite), Jersey, 14 March 1960, Mrs. F. Le Sueur.
Exposed slope above cliffs facing Bardsey Island, near Ffynnon Fair, Aberdaron, Lleyn Peninsula, Caerns.,
April, 1958.
- Holyhead Mountain, opposite South Stack, 31 Aug. 1954, D. E. Coombe (and later collections by M.C.F.P.).
Bare patches between wind-cut *Calluna* and *Erica cinerea*, on low rocky knoll between Clegyr Mawr farm
and the sea, near Llanrhyddlad, Anglesey, July 1955. Seedlings collected 1 April 1961.
- Summit of Three Castles Head, W. Cork, on open rocky ground (Devonian slates). Patches of more closed
vegetation (from which *T. guttata* is absent) with *Calluna*, *Erica cinerea*, *Cladonia* spp., 14 Aug. 1952,
S. M. Walters.
- Sloping bank, edge of pool below Three Castles Head, with *Calluna*, *Erica* and into marsh with *Drosera*,
Sphagnum, *Potamogeton polygonifolius* etc., 14 Aug. 1952, S. M. Walters.
- Bare patches in *Calluna* heath near summit of Middle Quarter Hill, Inishbofin, W. Galway, 14 Aug. 1958.
Rock outcrop in pasture near west end of Inishbofin, facing Inishark, 14 Aug. 1958.
- Dry short turf on cliffs above Baie des Trépassés on the Pointe du Van, near the Pointe du Raz, Finistère,
France, July 1952, C. D. Pigott.
- Sintra, Mercês, Estremadura, Portugal (from Estação Agronómica Nacional, Sacavém).
Roadside, Pe. da Sena, towards Sintra, Portugal, 12 Oct., 1957, I. A. Williams.