TRIFOLIUM OCCIDENTALE, A NEW SPECIES RELATED TO *T. REPENS* L.

By D. E. COOMBE
The Botany School, University of Cambridge

ABSTRACT

Trifolium occidentale is described as a new species related to but morphologically, genetically, cytologically and ecologically distinct from *T. repens* L. It is known in the British Isles from relatively dry coastal habitats in W. Cornwall and the Channel Islands. It occurs on the coast of N.E. Spain, and is probably widespread in W. and N.W. France. It is believed that it is not conspecific with *T. biasolettii* Steud. & Hochst., a little-known plant from Istria and Provence which may well be conspecific with *T. repens*.

INTRODUCTION

Trifolium repens L. is one of the most widespread and variable of the clovers and many infraspecific taxa have been described from wild populations, especially in the alpine and mediterranean regions of Europe (Rouy 1899, Ascherson & Graebner 1908, Gams 1924, Hayek 1927, Vicioso 1952, Hendrych 1956). The taxonomy and nomenclature of these populations remain confused in the absence of comprehensive experimental and cytological studies, since the copious agricultural literature on this important herbage plant refers in the main only to lowland populations of doubtful natural status, or to selected ' strains ' and cultivars which are largely self-incompatible and out-breeding. In meadows, pastures and lawns there is often a range of biotypes distinct in the shape and marking of the leaflets, in flower colour, in size, and so on : these are amenable to genetic analysis but not to orthodox taxonomic treatment.

The moist, fertile man-made pastures of the schists of the Lizard peninsula (W. Cornwall) are no exception in this respect, and even the natural climax grasslands of the windswept maritime clifftops on schists, serpentine and other rocks include diverse biotypes of what may well be truly wild plants which, although often smaller in flower and leaf than the cultivated ones, and although often with petioles and peduncles remaining prostrate even when grown in a glass-house, are nevertheless clearly referable to the variable species *T. repens*.

In September 1957, I became aware that the plant recorded as *Trifolium repens* in ' Rock Heath ' (i.e. species-rich *Festuca ovina – Calluna* heath on shallow pockets of soil among serpentine rocks of the Lizard peninsula; Coombe & Frost 1956) shows a combination of characters which separates it sharply from the populations of grasslands on deeper soils. Subsequently, a systematic search with L. C. Frost in 1958 of the coast of the Lizard peninsula from Mullion to Kennack showed that not only is this distinctive *Trifolium* widespread near the sea on both schists and serpentine where the soil is sufficiently shallow (less than 15 cm.), especially on rocky knolls or south-facing slopes on the exposed west coast, but that it is, in contrast to *T. repens*, remarkable for its lack of variability. The further discovery in early 1959 of identical plants (all near the sea) at St. Ives and Mousehole (W. Cornwall), and in both Jersey and Guernsey (Channel Islands), supported the idea that this is a distinct taxon, homozygous and probably inbreeding, and not hybridizing with *T. repens* despite the juxtaposition of the two where there is an abrupt change in soil depth from place to place.

The reasons for considering this new taxon as a species distinct from any described *Trifolium* are given later; meanwhile it is convenient to refer to it as *Trifolium occidentale*.

EXPERIMENTAL MATERIAL

Since clones of many perennial *Trifolium* species show much phenotypic variability depending on the time of year, age of the plant, and habitat (for example, dark pigmentation

is more evident in the winter and the degree of glaucousness depends on water balance and shading), ten clones of *T. occidentale* and eleven of *T. repens* for comparison were grown from comparable cuttings taken on 4 June 1959, potted up in large pans (Sankey No. 7) of John Innes compost, and kept in an unheated section (E3) of the Experimental Glasshouses at the Cambridge University Botanic Garden. During the winter and early spring the temperatures in this unheated section approximated to those in W. Cornwall. It cannot be claimed that all 21 clones grew under identical conditions because by the late spring of 1960 some of the *T. repens* clones had grown so vigorously that they were much more liable to dry out by the greater transpiration losses per pot; the plants themselves have a differential effect on their environment. In the field, of course, *T. occidentale* is the more liable to suffer drought because it grows on shallower soil than *T. repens.* Material has also been grown of both species collected from additional localities in the Channel Islands in March 1960, of *T. repens* collected from natural or semi-natural coastal habitats in Pembrokeshire and Wester Ross by H. L. K. Whitehouse in 1959 and 1960, and of *T. repens* from a number of European botanic gardens; but these plants have not been studied quantitatively.

The 21 clones studied in detail (with dates of the original collection in the field, and the underlying rock) are :

T. occidentale

O/KY Kynance, Lizard peninsula, W. Cornwall (September 1957; serpentine)*.
O/CA Caerthillian Cove, Lizard peninsula, W. Cornwall (June 1958; hornblende schist)* (Holotype); ‡ §.
O/GG Gew Graze, Lizard peninsula, W. Cornwall (June 1958; serpentine)*.
O/MU Mullion Cliff, Lizard peninsula, W. Cornwall (September 1958; serpentine)†.
O/EN Enys Head, Lizard peninsula, W. Cornwall (September 1958; serpentine)†.
O/MO Mousehole, nr. Penzance, W. Cornwall (January 1959; granite)* ‡.
O/IV The Island, St. Ives, W. Cornwall (January 1959; 'greenstone')* ‡.
O/GR Grandes Rocques, Guernsey, C.I. (April 1959; granite)† ‡.
O/PS Port Soif, Guernsey, C.I. (April 1959; blown sand over granite)† ‡.
O/JY Grosse Tête, Jersey, C.I. (April 1959; granite)† ‡.

T. repens

R/SW Canton du Pois, St. Bernard, Switzerland (Miss J. E. Tutin; June 1957).
R/LA Grassland C, Lakenheath Warren, W. Suffolk (July 1957, slightly calcareous sand).
R/GG Clifftop turf, Gew Graze, Lizard peninsula, W. Cornwall (September 1957; serpentine).
R/LU Lulworth Cove, Dorset (September 1957; Weald clay).
R/CA Caerthillian Cove, Lizard peninsula, W. Cornwall (June 1958; hornblende schist).
R/TR Tresco Flats, Scilly Islands, W. Cornwall (June 1958; acid blown sand).
R/IV The Island, St. Ives, W. Cornwall (January 1959; 'greenstone').
R/GY Cobo Bay, Guernsey, C.I. (March 1959; granite 'head' and loam).
R/GW Gweek, nr. Helston, W. Cornwall (Mrs. R. Henning, May 1959).
R/PO Poulsallagh, Burren, Co. Clare (June 1959; Carboniferous limestone).
R/YU Hajla, Yugoslavia (C. D. K. Cook, August 1959).

* Specimens pressed in June 1959 in **CGE, K, BM** and **G.**
† Specimens pressed in June 1959 in **CGE.**
‡ Specimens pressed in May 1960 in **CGE, K, BM** and **G.**
§ Specimens collected in the field at this locality in June 1958 in **CGE, K, BM** and **G.**

Diagnosis and description of Trifolium occidentale sp. nov.

The diagnosis and description are based on living plants of nine of the ten 'experimental' clones listed above (excluding clone O/PS) and therefore include clone O/CA,

from which both the specimen designated as the holotype and the isotypes were prepared, and eight other clones which I believe to be identical with O/CA. These nine clones are, I believe, identical with all but three individuals of the many thousands of plants of *T. occidentale* which I have examined in the field; the exceptions are clone O/PS from Guernsey and two further clones collected in Guernsey and Jersey in 1960, which differ in the pigmentation of the leaves.

Trifolium occidentale sp. nov. *T. repenti* ramis repentibus atque habitu generali similis; sed differt foliolis minoribus (fere 10 mm. × 10 mm.), crassioribus, subrotundis, vel obtusis vel emarginatis, glaucis, omnino immaculatis, marginibus vel cum dentibus paucioribus vel vix dentatis, nervis lateralibus in planta iam viva oculis nullo modo adjutis non translucentibus, paucioribusque, petiolis cum pilis flexuosis sparsis sed persistentibus praeditis, stipulis vini rubri colore, capitulis aliquantulum minoribus (fere 20–24 mm. latis) cum floribus lacteis paucioribus, 20 (–40) - floris, inodorisque, dentibus calycis in infima parte cum marginibus valde hyalinis, vel rectis vel convergentibus, duobus superioribus vel ovato-lanceolatis vel triangularibus et saepe in margine superiore 1–2 denticulis munitis, tribus inferioribus praedictis fere dimidio brevioribus, ovato-lanceolatis, vexillo corollae (cum ungue) 8–9 mm. longo.

Praecocius quam *T. repens* et florescit (a mens. Mart. exeunt. usque ad med. mens. Apr.) et deflorescit (a med. mens. Iun. ad med. mens. Quint.). In locis aridioribus calidioribusque habitat, in saxosis, in arenosis et in pascuis siccis, nunquam nisi in maritimis.

Holotypus in Herb. Univ. Cantab. (**CGE**) : Caerthillian Cove, near Lizard Town, W. Cornwall (v.c. 1), England; south-facing grassy slopes on shallow soil over hornblende schist, within 200 m. of the sea; altitude 20 m.; Clone O/CA, collected 23 June 1958; cultivated in Hort. Univ. Cantab.; pressed 3 June 1959. Isotypi in Herb. Bot. Reg. Kew (**K**), Herb. Mus. Brit. (Hist. Nat.) (**BM**), Herb. Cons. Bot. Genev. (**G**).

Similar to *T. repens* in general appearance, but differing in a remarkably constant combination of characters, some of which occur in populations or individuals of *T. repens*, but which together are highly characteristic of *T. occidentale*. Stems shorter than in most plants of *T. repens*, at most times green and glabrous, but sometimes reddish and sometimes very sparsely hairy, especially near the nodes. Leaflets dark green and glaucous *without light or dark markings*, *smaller* but *thicker* than in most plants of *T. repens*, rarely exceeding 10 × 10 mm., to 250 μ thick in sections of fresh material, mostly *orbicular* or very broadly cuneate at the base and slightly emarginate. Margin very narrowly hyaline, with *fewer*, less prominent teeth (becoming more prominent on drying), or sub-entire. Upper surface matt to the naked eye, minutely crystalline with a hand-lens, strongly papillose in transverse section under the microscope; lower surface very glossy. Lateral veins *fewer*, scarcely evident from above by reflected light, *not translucent* to strong diffuse light with the naked eye (in *T. repens* the lateral veins in fresh leaves appear colourless and translucent with the naked eye although they become opaque on drying). Petiole and petiolules with sparse but *persistent* flexuous, erecto-patent or patent, *colourless hairs* to 1 mm., especially at the time of flowering (less evident in the winter). Stipules deep vinous red, margins hyaline at maturity. Peduncles green, sparsely to densely clothed in colourless erecto-patent hairs ; pedicels conspicuously reddish on the upper side, sparsely hairy, about twice as long as the translucent, pinkish bracteoles at anthesis. Heads fewer-flowered than in most plants of *T. repens* : 40-flowered on well-developed heads, but often less (about 20) even on the same plant by the abortion of buds. Flowers creamy-white (never pinkish), *scentless*, after anthesis turning pale to dark brown (without any reddish tinge). Calyx green and slightly hairy at the base, the tube reddish on the upper side, the main veins red or green, the teeth green except at their red apices and at their conspicuously hyaline basal margins. The upper two calyx teeth ± parallel or convergent at anthesis, 1·5–2 mm. long, ovate-lanceolate or triangular, the base of each 1·5 mm. broad, *often with one or two prominent teeth on the upper margins*, the lower margin broadly hyaline at the base, the upper margins touching or overlapping at the base, so leaving no sinus. The lower three calyx teeth ± divergent, not much more than half the length of the others, 1·0–1·5 mm. long, ovate-

lanceolate, the hyaline margins meeting or overlapping at their widest part (0·75–1·0 mm.), slightly constricted at their bases. Standard 8–9 mm. long (including the claw), 4 mm. broad when flattened out, limb broadly elliptical, emarginate; wings exceeding the keel, notched or slightly toothed at the apex.

Nectar with ' more fructose and glucose than sucrose, whereas the type [*T. repens*] has a preponderance of sucrose ' (M. S. Percival *in litt.*, observations based on flowering material collected at Caerthillian Cove on 19 April 1959).

T. occidentale flowers earlier than *T. repens*, from late March or early April to the end of June or early July; and grows in drier, warmer places, on rocks, in dry pastures and sand dunes, always near the sea.

Variability of T. occidentale and T. repens

The greater variability of leaf size, shape and marking of *T. repens* is evident from Fig. 1. The mean length of ten terminal leaflets (each from a leaf subtending the first inflorescence on a stem) of 11 clones of *T. repens* ranges from 10·2 mm. (R/TR) to 22·2 mm. (R/CA), and the length/breadth ratio from 0·96 (R/GG) to 1·46 (R/YU; not illustrated), whereas for *T. occidentale* the corresponding ranges are 6·5 to 8·3 mm. long, and 0·90 to 0·95 length/breadth. Of course, ontogenetic drift in leaflet shape has been minimised by considering only physiologically equivalent leaves. Similarly, the maximum stem length (1 year's growth of plants in pans) varies more widely in *T. repens*, from 16 to 39 cm., but is only 6 to 12 cm. in *T. occidentale*. Also remarkable is the very great uniformity of coloration of the green* stems and dark vinous red stipules of *T. occidentale* in contrast to the

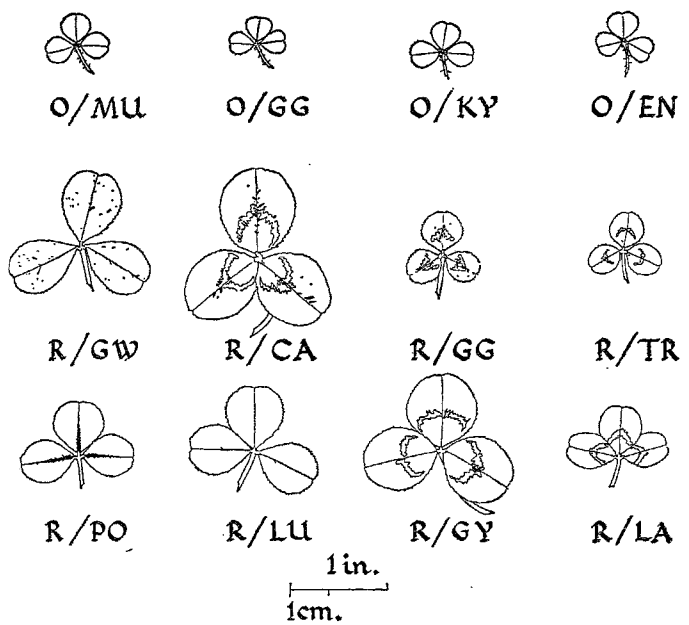

Fig. 1. Standard leaflets (see text) of four clones of *Trifolium occidentale* (top row) with neither light nor dark leaf markings, and of eight clones of *T. repens*, of which three have no light markings (R/GW, R/PO and R/LU) and two have no dark markings (R/GY and R/LA). Scale : × ½.

variation in *T. repens* in which the stems vary from green to bright or dark red, and the stipules from green to dark red veined. The length and erectness of the petioles also varies more in *T. repens* and there is clearly a selective advantage in the short, prostrate petioles of plants from extremely exposed clifftops (R/GG, 47 mm. long, R/PO, 51 mm. long)

* The stems may be reddish when the plants suffer drought.

compared with the long erect petioles (up to 129 mm.) of plants from thick *Festuca rubra – Dactylis* turf of more sheltered places. Petiole length of *T. repens* from formerly grazed grass-heath is intermediate (R/TR, 51 mm.; R/LA, 72 mm.). In *T. occidentale* petiole length varies from 37 to 59 mm. only (petiole measurements made at the same nodes as the leaflet measurements above).

Flower colour is also much more variable in *T. repens,* from pale creamy-white to the astonishingly deep, almost beetroot red of some of the plants ('var. *rubescens* DC.' of Clapham, Tutin & Warburg 1952), on Tresco Flats, Scilly Isles, where, however, the red-flowered population is clearly variable in colour and leaf-markings, R/TR being only one of a number of biotypes collected there in 1958.

So far I have found no evidence of genotypic variation in *T. occidentale* in W. Cornwall but there are two clones in Guernsey which deviate from the type. One (O/PS) forms a circular patch with marginal vigour, clearly derived from a single plant, in short sand-dune turf on the top of the 25 ft. (7·6 m.) knoll shown on the 3 in. map of Guernsey about 130 m. east of the Grandes Rocques Hotel, near Port Soif. This plant has obscure yellowish-white markings on the leaflets, but otherwise appears identical with *T. occidentale*; and as shown below, has the chromosome number, $2n = 16$, of this species. The other is a patch on the dunes about 170 m. further east-south-east and has dark markings along the lateral veins, but is otherwise typical *T. occidentale.* A hybrid origin of these two plants is unlikely in view of the chromosome numbers and breeding behaviour of *T. occidentale* and *T. repens*, and I have otherwise found no plants or populations intermediate between the two species despite their close proximity, and even intermixture, on soils of 15–20 cm. deep, in several places in Cornwall and Guernsey. A plant of *T. occidentale* from Le Pinacle, near L'Étacq, Jersey, collected in March 1960, has in cultivation scarcely glaucous, more yellow-green leaves than all the others; the 129 seedlings from an open-pollinated head of this clone all have the same coloration as the maternal parent. Otherwise it appears to be identical with other *T. occidentale.*

A consequence of the uniformity of *T. occidentale* is that each of the experimental clones, except O/PS, can be regarded as typical of the population from which it was collected, and with the exceptions mentioned, all the populations can be considered to belong to one biotype. In contrast, not only is the variation between localities very great in *T. repens*, as demonstrated, but each experimental clone is just one biotype arbitrarily selected from a genetically complex population : for example R/TR is one of a number of plants of various shades of pink and red flowers on Tresco Flats and R/GW is one of three biotypes collected by Mrs. Henning at Gweek. In some cases, however, the populations of *T. repens* appear to be more uniform in the field : R/GG, for example, seems to be the only biotype in very exposed cliff-top turf above Pigeon Ogo near Gew Graze; this may be accounted for by severe selection pressure in such extreme habitats.

Leaf anatomy

One of the most useful characters for distinguishing living *T. occidentale* is the opacity of the lateral veins of the leaflets in contrast to the nearly colourless translucence to the naked eye of those of *T. repens.* This, and the remarkable papillosity of the upper epidermis of *T. occidentale*, prompted an investigation of the leaf anatomy of the two species.

Serial sections, 16 μ thick, of the 21 clones were prepared from material collected and fixed in formalin-acetic-alcohol at the Botanic Garden on 24 October 1959. Permanent mounts stained in safranin and picric aniline blue were prepared. There was considerable shrinkage of the specimens, the mean thickness of the ten *T. occidentale* leaves being 156 μ, as opposed to about 250 μ in fresh material, but the two species showed consistent differences in structure and dimensions after preparation. O/CA and R/CA were selected for detailed study, and sections were cut at right angles to the lateral veins as well as to the main vein of the leaflets.

Fig. 2 shows the differences in structure in the region of a lateral vein between the two species. In *T. repens* the main lateral veins with their mechanical tissue (collenchyma or cellulose fibres) occupy two-thirds (or more) of the thickness of the mesophyll, and only a single layer of palisade intervenes between the vein and the upper epidermis, in which the

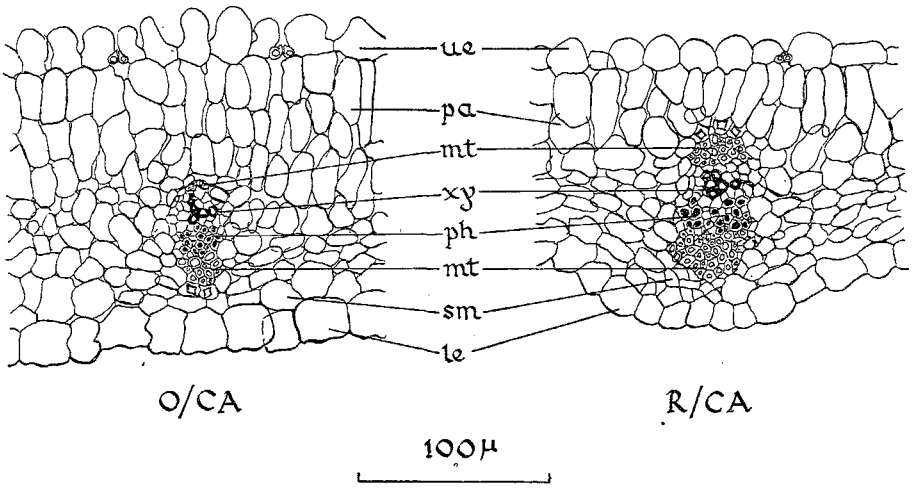

Fig. 2. Transverse sections (at right angles to the lateral veins) of leaflets of *Trifolium occidentale* (O/CA) and *T. repens* (R/CA); fixed and stained material. *ue*, upper epidermis; *pa*, palisade mesophyll; *mt*, mechanical tissue (bundle caps of collenchymatous appearance); *xy*, xylem; *ph*, phloem; *sm*, spongy mesophyll; *le*, lower epidermis. Scale : × 250.

cells are characteristically broader than high; whereas in *T. occidentale* the mechanical tissue is poorly developed on the adaxial side so that the whole vein occupies barely half the thickness of the mesophyll and three layers of palisade lie between the vein and the upper epidermis of which the cells are much higher than broad, having indeed a high conical or cylindrical form in section. The lower epidermis also tends to be thicker in *T. occidentale*.

There is, however, no absolute difference in the thickness of epidermis and mesophyll between the two species, although the total thickness of upper and lower epidermis is considerably less (mean 34 μ after preparation) in 10 out of 11 of the *T. repens* clones than it is in 9 out of 10 of the *T. occidentale* (mean 44 μ). The exceptional plants are R/PO, with a highly papillose upper epidermis, the upper and lower epidermis together totalling 44 μ, and O/PS which has the thinnest of the *T. occidentale* leaves and with a total epidermal thickness only 34 μ.

Leaf thickness and epidermal characters cannot, then, be regarded as diagnostic of *T. occidentale*, but the relation between the palisade and the lateral veins leading to the opacity of the latter appears to afford an important distinguishing character; indeed, in other sections prepared from pressed specimens of both species collected in the field the difference in development of the mechanical tissue is even more marked than in the sections of material grown in the glass-house.

PHENOLOGY

T. repens normally flowers from late May to September, but in 1959 *T. occidentale* was in full flower, both on granitic rocks and on sand dunes, in Guernsey on 2 April; and on south-facing slopes at Caerthillian Cove in W. Cornwall, where it had evidently been in flower for a few weeks already, on 18 April. By the beginning of July in 1958 and 1959 many plants of *T. occidentale* had finished flowering on the Lizard peninsula, and on 2 July 1959 some had ripe seed. In a warm glass-house at the Botanic Garden *T. occidentale*

O/CA had fully opened flowers on 15 March 1959 whereas *T. repens* R/CA had none until 27 April. The dates of flowering, however, depend very much on the age and vigour of the plants, so systematic observations were made in the spring of 1960 in the unheated glass-house on the 10 clones of *T. occidentale* and 11 of *T. repens* grown from comparable cuttings taken on 4 June 1959.

Table 1 shows that on the average the 10 clones of *T. occidentale* showed the tips of the earliest inflorescences on 14 March 1960, 46 days before *T. repens* (29 April); as the temperatures rose through April and May the differences between the two species became less. Even so, the first flowers were fully open, on the average, on *T. occidentale* 23 days before those on *T. repens* (24 April and 17 May respectively).

TABLE 1.

Mean dates of stages of flowering of 10 clones of *T. occidentale* and 11 clones of *T. repens* in a cold glass-house, 1960.

INFL = 1st inflorescence just visible beyond stipules.
TCEC = tip of corolla of most advanced flower just exceeding the calyx.
CFO = corolla fully open (anthers ripe).
CPA = corolla past anthesis (pedicel deflexed, corolla brown–*T. occidentale* – or pinkish–*T. repens*).

	INFL		TCEC		CFO		CPA
T. occidentale							
Mean date	14 March		18 April		24 April		4 May
Days from 1 March	13·6		48·6		55·0		64·8
Interval		35·0		6·4		9·8	
Standard deviation	7·6		3·3		3·2		2·3
s.e.m.	2·4		1·1		1·0		0·7
s.e.m. × 't' ($n = 9$, P = 0·05)	5·4		2·4		2·3		1·6
T. repens							
Mean date	29 April		13 May		17 May		26 May
Days from 1 March	60·4		73·5		78·4		87·6
Interval		13·1		4·9		9·2	
Standard deviation	8·4		7·1		8·4		6·5
s.e.m.	2·4		2·0		2·4		1·9
s.e.m. × 't' ($n = 10$, P = 0·05)	5·3		4·5		5·3		4·1
Difference (days) (*T. repens* – *T. occidentale*)	46·8		24·9		23·4		22·8

In the field in 1959 *T. occidentale* flowered earlier than in the glass-house, probably because of the higher near-surface temperatures on sunny south-facing slopes in the sunny coastal habitats than in the well-ventilated, unheated glass-house, whereas by mid-May the glass-house was much hotter by day than the normal habitats of *T. repens*, so this species flowered *later* out-of-doors.

The variability of *T. occidentale* is again rather small : all 10 clones opened their first flowers within 10 days (19–29 April), whereas the corresponding period for *T. repens* was 24 days (9 May–2 June).

None of the cuttings of the 10 plants of *T. occidentale* taken on 4 June 1959 subsequently flowered in that year, but all 11 cuttings of *T. repens* flowered before 4 October 1959. Similar observations have been made on these and other clones in 1958 and 1960.

In 1961 *T. occidentale* was flowering abundantly at Cudden Point near Perranuthnoe, W. Cornwall, on 3 April and, judging by the number of fully deflexed brown flowers, had

reached anthesis 10 days or a fortnight earlier. In a much warmer glass-house in 1961, all ten clones of *T. occidentale* flowered about 5 weeks earlier than in the cooler conditions of 1960.

COMMUNITIES

Thirteen 1 m². quadrats each containing *T. occidentale* (10 from the Lizard peninsula and 3 from the west coast of Guernsey) contain 102 species of vascular plants; four additional quadrats containing *T. repens* but no *T. occidentale* include a further 8 species. The lowest value of pH recorded (air-dry soils in 1:5 suspension; glass electrode) is 5·1

TABLE 2.

Constancy of *Trifolium occidentale* and *T. repens* and their associates in three noda based on sixteen 1 m². quadrats from the Lizard peninsula (W. Cornwall) and Guernsey (Channel Islands). Constancy on a scale of 1 to 4 for Noda 1 and 3, 1 to 8 for Nodum 2. For details of habitats, and additional species only occurring once in the sixteen quadrats, see the text. Species marked + also occur in Nodum 4.

Nodum No.	1	2	3
No. of 1 m². *quadrats*	4	8	4
+Festuca rubra	4	8	4
+Plantago lanceolata	4	8	4
+Hypochoeris radicata	3	8	4
+Leontodon taraxacoides	3	8	4
Armeria maritima	4	7	2
+Dactylis glomerata	1	8	4
+Daucus carota [1]	4	5	4
+Plantago coronopus	4	7	2
Aira caryophyllea	2	8	2
+Lotus corniculatus	2	6	4
Sedum anglicum	4	6	2
Holcus lanatus	1	6	4
+Koeleria cristata	1	7	3
Anthyllis vulneraria	3	4	3
Festuca ovina	2	5	3
+Cerastium atrovirens	3	5	1
Jasione montana	1	7	1
+Bellis perennis	1	4	3
Cynosurus cristatus	1	2	4
Sonchus oleraceus	2	2	2
+Cochlearia danica	2	2	1
Lolium perenne	2	2	1
+Ononis repens	1	1	2
Silene maritima	1	3	1
+Trifolium occidentale	4	8	–
+Bromus ferronii	4	6	–
Trifolium scabrum	3	4	–
Anagallis arvensis	1	1	–
+Catapodium marinum	4	1	–
Herniaria ciliolata	4	1	–
Aira praecox	2	–	1
Crithmum maritimum	2	–	–
Trifolium molinerii[2]	2	–	–
Scilla autumnalis	–	5	–
Erica cinerea	–	4	–
Trifolium subterraneum	–	4	–
Geranium molle	–	3	–
Trifolium micranthum	–	3	–
T. striatum	–	3	–
Calluna vulgaris	–	2	–
Filipendula vulgaris	–	2	–
Hypericum humifusum	–	2	–
Minuartia verna	–	2	–
+Poa pratensis[3]	–	2	–
Sagina procumbens	–	2	–
S. subulata	–	2	–
+Trifolium dubium	–	2	–
Betonica officinalis	–	1	4
Trifolium pratense	–	–	4
T. repens	–	–	4
Viola riviniana	–	–	4
Carex flacca	–	–	3
Crepis capillaris	–	1	3
Prunella vulgaris	–	–	3
Scilla verna	–	1	2
Ulex europaeus	–	1	2
+Ranunculus bulbosus	–	6	4
Luzula campestris	–	5	4
Agrostis tenuis	–	4	4
Anthoxanthum odoratum	–	5	3
Galium verum	–	4	3
+Thymus drucei	–	4	3
Centaurium erythraea	–	4	2
Achillea millefolium	–	2	3
Carex caryophyllea	–	3	2
Plantago maritima	–	2	3
Rumex acetosa	–	2	3
Cerastium holosteoides	–	2	1
Cirsium vulgare	–	2	1
Polygala vulgaris	–	2	1
Chrysanthemum leucanthemum	–	1	1
Agrostis stolonifera	1	–	1

1 Mostly referable to subsp. *gummifer* Hook. f.
2 In my view better regarded as *T. incarnatum* L. subsp. *molinerii* (Balb.) Hook. f.
3 Probably includes *P. subcaerulea* Sm.

on hornblende schist; the highest values are 7·1 on ' greenstone ' and 7·4 on blown sand (with shells).

The 17 quadrats, which all lie within 800 m. of the sea and below 60 m. altitude, are closely related floristically, with *Plantago lanceolata*, *Hypochoeris radicata*, *Leontodon taraxacoides* and *Festuca rubra* occurring in 16 or 17 of them, but they can for convenience be divided into four characteristic ' noda ' (*sensu* Poore, 1955), each with a number of characteristic ' constant ' species; even so, intermediates between these noda occur in many places.

Table 2 lists the species occurring in 2 or more of the 16 quadrats comprising 3 of the noda (excluding the nodum on blown sand). In every case percentage cover was recorded, but since 7 years' observation of permanent quadrats in similar communities on the Lizard peninsula shows that the cover of most species varies within very wide limits from year to year whereas the species list for any 1 m². quadrat remains fairly stable, only constancy is given in Table 2.

The four noda distinguished are :

1. The *Trifolium occidentale – Herniaria ciliolata – Catapodium marinum* nodum.

Four quadrats from near high water mark on rocky, exposed western coasts, characterized floristically by the constancy of *Herniaria ciliolata* and *Catapodium marinum* and the occurrence of *Trifolium molinerii* and *Crithmum maritimum*. The soil is very shallow, not more than 10 cm., over granite (Guernsey) or hornblende or mica schists (Lizard). The cover of living vascular plants is never complete (25–85%) and erosion of the soil is often severe. The nodum is only developed on south- to west-facing slopes of 10 to 15°, fully exposed to wind and salt spray. The differences between Guernsey and Lizard lists are very small : *Polycarpon tetraphyllum* does not occur in this habitat at the Lizard, and *Trifolium molinerii* is not known from Guernsey. At the two Jersey stations for *T. molinerii* there is no *T. occidentale*. This nodum depends for its maintenance on severe exposure and the shallow soil; it is independent of grazing and burning. The soil pH ranges from 5·9 to 6·5.

Quadrats (the code number of a clone indicates that it was collected in the quadrat).

1 (a). South side of the Grandes Rocques peninsula, Guernsey, just above high water mark; granite; pH 6·1. Additional species ; *Cynodon dactylon*, *Polycarpon tetraphyllum*, *Sagina maritima*, *Senecio vulgaris* var. *radiatus*. (O/GR).

1 (b). South slopes of the cairn north of Caerthillian Cove, Lizard, W. Cornwall, altitude 20 m., fully exposed to the sea : hornblende schist; pH 5·9. Additional species : none.

1 (c). South-west slopes of the spur between the two valleys, Caerthillian Cove, alt. 15 m., fully exposed; hornblende schist; pH 6·5. Additional species : *Sagina ciliata*.

1 (d). West-facing cliff slope above Crane Ledges, Lizard, fully exposed, alt. 15 m.; mica schist; pH 6·3. Additional species : *Spergularia rupicola*.

2. The *Trifolium occidentale – Scilla autumnalis – Jasione montana* nodum.

Eight quadrats, less exposed than the last, extending to 800 m. from the sea and to 60 m. altitude. The soil is less shallow – up to 15 cm. deep – on south-east, south or westerly slopes of 3 to 30° over granite (Guernsey) or hornblende schist or serpentine (Lizard). The cover of vascular plants ranges from 50 to 90%. In some places cattle-grazing is heavy; rabbits were numerous until 1954. Even in the absence of grazing, periodic droughts (e.g. 1949, 1955, 1959) decimate *Calluna*, *Erica cinerea* and *Festuca ovina* and leave the community open to a large number of drought-resistant and opportunist species. On deeper soils, especially in rock crevices, *Calluna* and *Erica cinerea* survive droughts but disappear under heavy grazing. Burning is insignificant as an environmental factor. Again there are few significant differences between quadrats regardless of parent rock or location : *Isoetes histrix* and *Chamaemelum nobile* (*Anthemis nobilis*) were only found growing with *T. occidentale* in Guernsey,* although they both occur widely in spots moist in the winter on both

* *T. occidentale* has recently (April 1961) been found growing with *Isoetes* and *Chamaemelum* on serpentine at the Lizard near The Rill.

schist and serpentine on the Lizard peninsula; but *Minuartia verna* and *Filipendula vulgaris* do not occur on the schists.

This nodum lacks the extreme maritime element of Nodum 1, although *Armeria maritima* and *Daucus carota* (including subsp. *gummifer*) are still constant, but the sub-mediterranean element is augmented by therophytes such as *Trifolium subterraneum* and geophytes such as *Isoetes histrix* and *Scilla autumnalis* – this last not occurring in the other noda considered here. In addition, many pasture species come in, e.g. *Dactylis glomerata*, *Ranunculus bulbosus* and *Luzula campestris*; some of these, e.g. *Galium verum*, have often been observed to suffer severe damage from salt-laden winds in more exposed places, but this species is highly resistant to droughts which kill *Calluna* and *Festuca ovina*. The measured soil pH values range from 5·1 to 6·2.

T. occidentale occurs in similar communities, but less rich in species, on ' greenstone' (diabase) or epidiorite at Cudden Point (pH 6·9) and near Bessy's Cove (pH 5·5) in Mount's Bay, W. Cornwall.

Quadrats

2 (a). South side of the Fort Hommet peninsula, Guernsey; a relatively sheltered spot with seepage of moisture in winter, similar to *Isoetes histrix* habitats on the Lizard peninsula, alt. 10 m.; granite; pH 5·9. Additional species : *Isoetes histrix*, *Chamaemelum nobile*, *Erodium cicutarium*.

2 (b). Top of Mullion Cliff, Lizard, away from the cliff edge, alt. 60 m.; serpentine; pH 6·2; essentially ' Rock Heath ' (Coombe & Frost 1956) modified by cattle-grazing, and by rabbits in the past. Additional species : none. (O/MU).

2 (c). Enys Head, on the relatively sheltered east coast of the Lizard peninsula, alt. 45 m.; serpentine; pH 6·1. Additional species : *Senecio jacobaea*, *Trifolium arvense*. (O/EN).

2 (d). Kennack Cliff, on the east side of the Lizard peninsula, alt. about 50 m.; serpentine. Additional species : *Sieglingia decumbens*.

2 (e). Rock outcrop east of the ' British Village ' at Kynance Gate, Lizard, 800 m. from the sea, altitude 60 m.; serpentine; pH 6·2. Additional species : *Polypodium vulgare*, *Umbilicus rupestris*. (O/KY).

2 (f). Summit of Carn Caerthillian, Lizard, 220 m. from the sea, altitude 45 m.; serpentine. Additional species : *Beta vulgaris* subsp. *maritima*, *Aphanes microcarpa*, *Vulpia bromoides*, *Vicia angustifolia*.

2 (g). South-facing slope of the main valley, Caerthillian Cove, Lizard, relatively sheltered, altitude 20 m.; hornblende schist. Additional species : *Euphrasia occidentalis*. (O/CA).

2 (h). North-west facing slope of the spur, Caerthillian Cove, altitude 20 m.; hornblende schist; pH 5·1; exceptional for the occurrence of *Herniaria* on a northern aspect, and transitional to Nodum 3. Additional species : *Trifolium ornithopodioides*, *Taraxacum officinale*.

3. The *Cynosurus cristatus – Betonica officinalis* nodum.

On the hornblende schist on the Lizard peninsula both north- and south-facing slopes (10 to 27° in the four quadrats) on deep moist soils (20 cm. or more) support, under heavy cattle grazing and in situations relatively sheltered from the sea, a closed turf (95 – 100% cover) rich in mesophytic perennial herbs and grasses, with few therophytes. *T. occidentale* is absent from this nodum, but both *T. repens* and *T. pratense* are constant, and it is very similar to the pastures on non-calcareous soils described from Ireland by Braun-Blanquet & Tüxen (1952) as the *Cynosurus cristatus – Centaurea nigra* Association. The Lizard nodum, however, differs notably in the abundance and constancy of *Betonica officinalis* and the absence of *Senecio jacobaea*; the local abundance of *Plantago maritima* is also remarkable. No less than 43 species are common to this and Nodum 2, and every gradation between them can be found in the field following variations in soil depth and moisture;

indeed one quadrat listed in 1958 contained both *T. occidentale* and *T. repens*; the soil depth in this quadrat varied between 16 and 22 cm. The pH of the only soil sample collected from the four quadrats is 6·1; but generally it varies between 5·1 and 6·5 in similar closed turf, the higher values occurring in flushed soils, or nearer the sea; lower values on leached knolls, or away from the sea.

Quadrats

3 (a). North-facing slope of the spur, Caerthillian Cove, Lizard, relatively sheltered although the sea is only 40 m. away, altitude 20 m. Additional species : *Ranunculus ficaria.*

3 (b). 10 m. west of 3 (a) and 4 m. below. Additional species : none.

3 (c). South-facing slope of the main valley, Caerthillian Cove, on deep, moist soil, sheltered, altitude 20 m. Additional species : *Ranunculus acris.*

3 (d). North-facing slope of the south valley, Caerthillian Cove, relatively sheltered, altitude 20 m.; pH 6·1. Additional species : *Centaurea nigra.*

4. The *Trifolium occidentale–Bupleurum baldense* nodum.

Near Port Soif and Portinfer, just north of Grandes Rocques, Guernsey, *T. occidentale* is frequent on the south-facing slopes of the rather stable coastal sand-dunes; *T. repens* also occurs, but usually in moister hollows or on north-facing slopes. In a 1 m². quadrat at Port Soif there were 39 species of vascular plants on a southerly slope of 15° with 70% vascular plant cover; 25 species (those marked + in Table 2 and in the list below) occur in Noda 1 and 2; the other 14 include widespread dune species (e.g. *Medicago lupulina*, which frequently occurs on Cornish dunes with *T. occidentale*) and many therophytes characteristic of the Channel Islands sand dunes. The strict calcicoles which occur elsewhere in Guernsey and Jersey (e.g. *Poterium sanguisorba*) are absent, although the pH in this quadrat is 7·4 and abundant snails occur.

Additional species in Nodum 4

Agropyron junceiforme
Arenaria serpyllifolia
Bupleurum baldense
Carex arenaria
Cerastium semidecandrum
Diplotaxis tenuifolia
+Erodium cicutarium
Medicago lupulina
Mibora minima
Phleum arenarium
+Polycarpon tetraphyllum
Raphanus maritimus
Saxifraga tridactylites
Sedum acre
+Senecio vulgaris var. radiatus
Silene conica
+Taraxacum officinale
Veronica arvensis
+Vicia angustifolia

On the north-east side of Port Soif, *T. occidentale* grows in the *Ammophila* zone on less stable dunes with *Matthiola sinuata* and *Lagurus ovatus*. It has not been seen on the extensive dunes of St. Ouen's Bay, Jersey, despite its occurrence on the cliffs nearby at L'Étacq but in Cornwall it occurs abundantly on blown sand, usually with *Festuca rubra* dominant and sometimes mixed with *T. repens*, at Gunwalloe Church Cove, where it was detected by Mrs. R. Henning, at Prah Sands (pH 7·4) and in many places between the railway and the sea from Marazion to Penzance (pH of a sample near the *Cynodon* locality at Marazion 6·5).

Bryophytes and lichens

Nodum 1. Except for *Xanthoria parietina, Ramalina scopulorum* and other saxicoles on the rock outcrops they are not important and sometimes absent.

Nodum 2. Hypnum cupressiforme and *Cladonia rangiformis* are the most constant species, although their cover rarely exceeds a few per cent. The submediterranean element is not as pronounced as in some other of the Lizard and Channel Islands communities : *Scleropodium illecebrum, Scorpiurium circinatum* and *Riccia beyrichiana* occur rarely. The other species are more widespread ones : *Bryum caespiticium, Weissia microstoma, W.*

controversa, Dicranum scoparium, Frullania tamarisci, Metzgeria furcata, Porella laevigata, Camptothecium sericeum, Trichostomum brachydontium, Cladonia pyxidata and *Peltigera* sp.

Nodum 3. Where the vascular plant cover is 100% the lush turf contains no bryophytes or lichens, but on the more open, steep north-facing slopes, especially where there is micro-terracing, the bryophytes include *Fossombronia angulosa, Scapania curta, Saccogyna viticulosa, Eurhynchium striatum, Dicranum bonjeani, Mnium hornum* and *Rhynchostegiella pallidirostra,* which never occur on unshaded south-facing slopes.

Nodum 4. The only bryophyte in the one listed quadrat was *Tortula ruraliformis* (cover 25%), but *Pleurochaete squarrosa* is widespread on the Channel Islands dunes, as at Kennack Sands and elsewhere on the Lizard peninsula.

Distribution

The following list summarises the localities for *T. occidentale* given under ' Experimental material ' and ' Communities,' and includes further records. In all cases I have verified the identifications personally. I have seen the plant at undated localities in both 1959 and 1960.

Isles of Scilly : Peninnis Head, St. Mary's (granite), ' in short turf near the light-house,' and ' seen also on St. Agnes and Gugh in similar habitats,' Mr. and Mrs. D. L. Vercoe (per Mrs. Evelyn Almond), 1961.

W. Cornwall : Godrevy Towans, ' on clayey soil,' R. C. L. Howitt, 1959 : The Island, St. Ives, ' greenstone,' 1959; Sennen, R. C. L. Howitt, 1959; Mousehole, granite, 1959; Penzance to Long Rock, blown sand and shingle, 1961; Marazion, blown sand, R. Jefferies and L. C. Frost, 1960; Cudden Point, ' greenstone,' 1961*; Prussia Cove, Bessy's Cove and Hoe Point, shales, 1961; Prah Sands, blown sand, 1961; Halsferran Cliff, shales, 1960; Gunwalloe Church Cove, blown sand, 1960; Poldhu Cove, shales, 1960; Mullion Cliff, serpentine; Pedn Crifton, hornblende schist; Pol Cornick, Vellan Head, Gew Graze, The Rill, the British village at Kynance, Yellow Carn, Carn Caerthillian, the last seven localities all on serpentine; Caerthillian Cove, on hornblende and mica schists; Enys Head, serpentine; Eastern Cliff, Kennack, serpentine.

Guernsey : Portinfer, blown sand; Port Soif, blown sand; Grandes Rocques, granite; Fort Hommet, granite; Jerbourg Point, granite.

Jersey : Le Pinacle, near L'Étacq, granite, 1960; Grosse Tête, granite, 1959.

T. occidentale probably occurs in many more coastal localities on the Land's End peninsula and on the north coast of W. Cornwall, but I cannot find it between Eastern Cliff, Kennack, and Coverack on the east coast of the Lizard peninsula. M. J. E. Coode cannot find it at Dodman Point, W. Cornwall, and H. L. K. Whitehouse has looked without success in the extreme south of Devon, in Pembrokeshire, and in Wester Ross and Sutherland. However the plant was almost impossible to detect for nearly a year after the severe drought of 1959 even in known localities.

Dr. E. W. Davies (Mrs. E. W. Woodward) has collected a plant identical with *T. occidentale* in N.W. France, where it is probably widespread, and Mr. J. P. M. Brenan has drawn my attention to two sheets from N.E. Spain in the Herbarium at Kew which we agree are probably identical with British *T. occidentale.* These are ' *T. prostratum* Bias., *Gandoger, Fl. Hisp. exsicc.* 77, April 1895, Pasajes, Guipuzcoa ' and ' *T. repens β microphyllum, Gandoger, Fl. Hisp. exsicc.* 60, April 1895, S. Sebastian, Guipuzcoa.' (Pasajes is on the coast 4 km. east of S. Sebastian). These Spanish specimens have the very characteristic calyx, petiolar hairs and leaflet shape of *T. occidentale*; as in that species the stipules appear to have been red and the leaflets unmarked, while the adaxial mechanical tissue of the lateral veins is less well developed than in *T. repens.* The early flowering and coastal localities also correspond with *T. occidentale.* Mr. Brenan agrees that these two Spanish sheets are not the same as European specimens labelled *T. biasolettii* Steud. & Hochst. (= *T. prostratum* Bias.), an obscure taxon probably conspecific with *T. repens* (see pp. 83–86).

* Specimens pressed in April 1961 in **CGE, K, BM** and **G.**

THE EFFECTS OF DROUGHT AND ON-SHORE GALES

Acquaintance with the vegetation of the Lizard peninsula at all seasons of the year over the last ten years makes it plain that the habitats of *T. occidentale* are much more liable to severe desiccation than those of *T. repens*. Even in normal summers this is particularly apparent at Caerthillian Cove where after a hot dry spell the shallow soil of the *T. occidentale – Herniaria – Catapodium* and *T. occidentale – Scilla autumnalis – Jasione* noda on the south-facing slopes is dry and powdery and the vegetation crisp and brown, whereas in adjacent *Cynosurus – Betonica* areas with *T. repens*, both on south- and north-facing slopes, the much deeper soil, which has a good crumb structure, remains moist and the vegetation green, or bright with flowers of *Betonica* and *Leontodon taraxacoides*. During the autumn and winter the *T. occidentale* noda become green again, *Plantago coronopus* in particular contributing largely to the sward. After the very hot dry summers of 1949, 1955 and 1959 drought effects were more severe and persistent, with the wholesale death of *Calluna* and *Festuca ovina* on the shallow ' Rock Heath ' soils, and even the *Cynosurus – Betonica* nodum suffered a temporary diminution in the more mesophytic species. The heat and drought of 1959 were exceptionally prolonged, and their effects have been very striking, particularly in contrast to the very wet summer of 1958. A certain 1 m². quadrat at Caerthillian Cove had 60% cover of *T. repens* in June 1958; in July 1960 there was none, nor could I find *T. repens* (R/GG) in the clifftop turf near Gew Graze. On the granite at Grandes Rocques in Guernsey large patches of vigorous *T. occidentale* photographed in flower in early April 1959 were reduced to a few scraps of stem and leaf by March 1960, while at Jerbourg Point I could find only a few persistent stems and one seedling. On the sand-dunes north-east of Grandes Rocques the drought effects were much less apparent, although even there *T. occidentale* was reduced in area and vigour. In Jersey in March 1960 I could find only a few plants on *north-facing* slopes near Le Pinacle, and none at all on the burnt-up south-facing slopes. In June and July 1960 I saw only one withered inflorescence on the whole of the Lizard peninsula (although every locality then known was examined carefully), in a deep rock-crevice at Caerthillian Cove, while in many of the permanent quadrats set up in 1958 the plant was invisible. However in others there were a few wilted seedlings with 2 or 3 leaves (the latter half of June 1960 was again hot and dry at the Lizard before the long wet period set in). Despite the wholesale decimation of established plants, *T. occidentale* can clearly maintain itself in much drier habitats than *T. repens*. In pans in the glass-house it wilts much less readily than *T. repens*, but this may in part be due to the less rapid loss of water from the *T. occidentale* plants, which after 10 to 12 months' growth from cuttings have a much smaller total leaf area per pan.

The recovery of *T. occidentale* on the Lizard peninsula during the wet period July to September 1960 was very striking. At Enys Head, where in a particular rock crevice there were only nine small wilted seedlings on 1 July (all the old plants having died and disappeared), there were many vigorous plants 20 cm. in diameter and numerous seedlings at all stages of growth on 28 September; these were beginning to flower on 2 April 1961. *T. repens* showed a similar recovery on deeper soils in September at Gew Graze and in the quadrat at Caerthillian Cove where in June 1960 it was invisible.

T. occidentale is much more resistant to the adverse effects of on-shore gales than most *T. repens*. In early April 1959 a spell of strong westerly winds was followed by the wholesale browning of the leaves of *T. repens* (R/GY) in coastal turf on deep soil in Cobo Bay on the west coast of Guernsey, whereas nearby *T. occidentale* on dry rocky knolls, if anything even more exposed to wind and spray, was apparently unharmed and continued to flower. R/GY is, however, a plant with conspicuously long erect petioles and large leaves; possibly the smaller-leaved *T. repens* from exposed cliffs with prostrate (R/GG) or semi-prostrate (R/PO) petioles, or with a thicker, more papillose upper epidermis like that of *T. occidentale* would suffer less damage.

T. occidentale must also tolerate high sodium chloride concentrations in the soil, especially in the *T. occidentale – Herniaria – Catapodium* nodum, where it is associated near high water mark with such plants as *Crithmum* and *Spergularia rupicola*. R. L. Jefferies

has found 11·0 m.e./100 g. air-dry soil exchangeable sodium in soil samples collected by L. C. Frost from the *Herniaria – T. occidentale* quadrat 1 (d) by the sea just south of Caerthillian Cove (exchangeable potassium 2·3, calcium 22·3, magnesium 24·0 m.e./100 g., sodium forming, as m.e., 18% of the exchangeable cations determined, magnesium 40%).

Chromosome number

Among the bracteolate clovers of *Trifolium* subgenus *Trifoliastrum* to which *T. repens* belongs the chromosome number is most commonly $2n = 14$ or 16, although 28 is reported for *T. dubium* and both 14 and 32 for *T. micranthum* (Clapham, Tutin & Warburg 1952; Darlington & Wylie 1955). The most frequently reported number in *T. repens* is $2n = 32$, more rarely 48, with 64 in spontaneous or induced autopolyploids (Atwood 1944; Darlington & Wylie 1955; Pandey 1957); $2n = 16$ has not been reported in this species.

Chromosome counts on root tips of *T. occidentale* were made by M. J. E. Coode and M. J. Swift during July and August 1960. Squashes stained with aceto-orcein gave at least one unambiguous count of $2n = 16$ in each of the experimental clones : O/AC, O/GG and O/KY from W. Cornwall; O/GR and O/PS (with light markings on the leaves) from Guernsey; and O/JY from Jersey. Another plant from Port Soif, Guernsey, collected in March 1960, also gave $2n = 16$, while in May 1960 I had seen about eight bivalents in pollen-mother-cells in a plant from Le Pinacle, Jersey.

In contrast Coode and Swift found $2n = 32$ in root tips of *T. repens* from W. Cornwall (R/CA), while in R/GG and R/GY the number appeared to lie between 26 and 36, but clear preparations were not obtained of these two clones. Nevertheless, this range is consistent with the published number of 32, and my Cornish *T. repens* plants clearly differ from *T. occidentale* from adjacent localities with its uniform 16.

Self-compatibility and homozygosity of T. occidentale

In the spring of 1959 a pan of *T. occidentale* from Caerthillian Cove, from which the clone O/CA was later grown, flowered in a *warm* section of the glass-house earlier (15 March) than the others in a cool section. The early inflorescences nevertheless produced viable seed, suggesting that the plant is self-compatible, but proof was lacking as the pan may not have contained a single clone. The seed from one early inflorescence produced 30 seedlings identical with each other and with the maternal plant in vegetative and floral characters, suggesting a considerable degree of homozygosity.

The plants grown from cuttings in 1959 were used in 1960 to test these tentative conclusions. Six clones of *T. occidentale* (O/CA, O/IV, O/MO, O/GR, O/PS, O/JY) were placed in muslin cages on 8 May after any inflorescences with corollas visible and any shoots trailing over the sides of the pans had been cut off. Unfortunately, with this treatment many of the young inflorescences aborted : their peduncles bent over at the apex and the young flower buds yellowed and died. The few inflorescences that matured were few-flowered with most of the central (distal) buds abortive. The petioles lengthened excessively and the stems reddened. In the circumstances it is surprising that any seed developed. In the caged plants some of the surviving heads were self-pollinated by hand, using wedges of stiff paper to ' trip ' the flower and rub pollen on the stigma; others were carefully left untouched to see whether they were effectively autogamous. The other four clones of *T. occidentale* and the eleven of *T. repens* were left uncovered and intermixed on the bench, but heads of some were bagged in transparent paper envelopes. Bumble-bees (*Bombus* spp.) frequently visited the unbagged, uncaged flowers, and when both *T. occidentale* and *T. repens* were in flower (late May to early July) they often pollinated each species in turn. Observations were also made on three plants collected in March 1960 in the Channel Islands: these were not grown from single shoots but it is very likely that each consists of a single clone.

Ripe seeds from one open-pollinated head of each of the plants on the open bench and from all the self-pollinated heads were sown in the glass-house, warm in winter, between 24 and 27 July 1960. Some *T. occidentale* seed germinated very rapidly : up to 50% in 2 weeks and 100% in 3 weeks in a few cases. *T. repens* in general was much slower, only R/LA approaching 25% in 3 weeks, the majority giving only 0 to 5% after six months. Some of the *T. occidentale* also produced few or no seedlings within this period.

Despite the obviously deleterious effects of the cage treatment on *T. occidentale*, and the possibility that bagging depresses seed development in both species, the data in Table 3 indicate that

(a) in two wild *T. repens* clones there is a very high degree of self-incompatibility, but much seed is set with open pollination, and

(b) in *T. occidentale* (i) there is self-compatibility to a greater or lesser degree in at least 7 clones and three other plants, (ii) self-fertilization is effective in unmanipulated

TABLE 3.

Numbers of seed per head (24–27 July 1960) and numbers of seedlings (31 January 1961). Unless otherwise stated, all seedlings from one head are phenotypically identical with each other and with the female parent.

T. occidentale	
O/KY	Open-pollinated : 92 seeds; 12 seedlings.
O/CA	Three heads hand-selfed in cage : 2 of these aborted, the other produced 29 plump seeds; no seedlings. One head not manipulated in cage : 31 plump seeds; 1 vigorous seedling with 5 inflorescences just visible on 31 January.
O/GG	Open-pollinated : 105 seeds; 58 seedlings.
O/MU	Open-pollinated : 90 seeds; 13 seedlings plus some just germinating.
O/EN	Open-pollinated : 92 seeds; 23 seedlings. Bagged : 59 seeds; 30 seedlings plus some just germinating.
O/MO	Three heads hand-selfed in cage : 2 aborted, the other produced 1 seed (not sown). One head not manipulated in cage : 14 seeds; 2 seedlings.
O/IV	One head hand-selfed in cage : 9 seeds; 6 seedlings.
O/GR	Three heads hand-selfed in cage : 2 aborted, the other produced 11 seeds; no seedlings. One head not manipulated in cage : 25 seeds; 2 seedlings.
O/PS	(This is the clone with yellowish-white markings on the leaves; all 17 seedlings show the parental leaf-marking). Two heads hand-selfed in cage : 5 and 6 seeds; 7 seedlings, 1 with 1 inflorescence just visible. Three heads not manipulated in cage : 5, 3 and 3 seeds; 10 seedlings, 1 with inflorescence just visible.
O/JY	Three heads hand-selfed in cage : 2 rotted, 1 no seed. One head not manipulated : 20 seeds; 1 seedling with 1 inflorescence just visible. Port Soif, Guernsey, 1960. (This plant has the dark flecks along the lateral veins of the leaflets). Open-pollinated : 70 seeds; 37 seedlings with dark flecks, 18 apparently unmarked and appearing identical with typical *T. occidentale*. Bagged : 4 seeds; 3 seedlings with dark flecks, 1 unmarked. Port Soif, Guernsey, 1960. (This is another typical *T. occidentale* from blown sand). Open-pollinated : 155 seeds; 61 seedlings. Le Pinacle, Jersey, 1960. (This is the plant with paler green leaves than the type). Open-pollinated : 152 seeds; 129 seedlings (all pale green like the female parent; some heavily infected with *Uromyces* cf. *flectens*). Bagged : 5 seeds; 5 seedlings, all like the female parent.
T. repens	
R/CA	Four bagged heads : no seed in any. Open-pollinated : 106 seeds; no seedlings.
R/GY	Three bagged heads : no seed in any. Open-pollinated : 119 seeds, no seedlings.

(Other *T. repens* clones : generally about 100 seeds per open-pollinated head, but an average of about 25 in R/TR, R/PO and R/YU and only 4 in R/SW; no germination in 6 months in most).

plants, (iii) all typical (with unmarked and dark green leaves) *T. occidentale* shows a very high degree of homozygosity for all characters obvious in the seedlings, (iv) the pale-leaved plant from Le Pinacle, Jersey, also shows a high degree of self-compatibility and homozygosity, (v) the dark-flecked plant from Port Soif, Guernsey, segregates into flecked and unflecked progeny whether bagged or open-pollinated, the unflecked F_1 being phenotypically indistinguishable from typical *T. occidentale*,* (vi) the plant with yellowish-white leaf markings shows no segregation in the 17 selfed seedlings and is probably homozygous for this character, (vii) within the limitations of the observations there is no evidence of gene-flow from *T. repens* to *T. occidentale* despite the opportunities provided for cross-pollination by bees in the open-pollinated plants, all seven open-pollinated *T. occidentale* producing progeny phenotypically similar to the maternal parent, and (viii) there is no positive evidence, at least in the F_1, of gene-flow within *T. occidentale*, since neither dark flecks nor pale leaves appeared in the open-pollinated progeny of unmarked parents; but of course we do not know whether these characters in *T. occidentale* are dominant to unmarked or ' solid ' leaves as they are in *T. repens* (Atwood 1942).

Taxonomic rank

Specific rank has been given in the past to so many European taxa which are mostly regarded as synonymous with *T. repens* L. (see, for example, Ascherson & Graebner (1908), Gams (1924), Vicioso (1952)) that convincing reasons must be found for giving a binomial to a taxon clearly closely related to this variable and wide-ranging plant. Behind all the various concepts of the species lies the idea of genetic and morphological continuity within the species and discontinuity between species, but the barriers to gene flow between populations are so diverse qualitatively and quantitatively in plants that it is largely a matter of convenience which determines whether a population should be given specific rank.

A ' good ' species should be readily identifiable in the field and preferably also in the herbarium, even although many valuable diagnostic characters may be lost in the processes of pressing and drying, particularly pigmentation, scent and taste, and habit of growth. *T. occidentale* is not easy to distinguish in dried material from all plants of *T. repens*, but the ease with which many botanists to whom I have shown the plant in the field have been able subsequently to identify it in new localities encourages me to believe that it is morphologically distinct from all British *T. repens* at least. This belief and the distinct distribution of *T. occidentale* would justify its consideration as a geographic subspecies; but the apparent absence of any hybrids in the field and the evidence that it is cytologically distinct suggest that it is best regarded as specifically distinct from *T. repens*. The case for this is quite as strong as for the specific separation of *T. dubium* Sibth. and *T. micranthum* Viv., or *T. campestre* Schreb. and *T. aureum* Poll., and certainly much stronger than for separating *T. molinerii* Balb., and *T. incarnatum* L., while among the close relatives of *T. repens*, the alpine *T. pallescens* Villars and *T. thalii* Schreb. are generally regarded as species on grounds no stronger than those for *T. occidentale*.

The problem of T. biasolettii Steud. & Hochst.

There remains the possibility that *T. occidentale* is conspecific with some extra-British *Trifolium* related to *T. repens*. *T. pallescens* and *T. thalii* are both glabrous and non-creeping, and differ widely from *T. occidentale*, although *T. thalii* has $2n = 16$ (Darlington & Wylie 1955) and it would be interesting to know if it will hybridise with *T. occidentale*. This leaves only *T. biasolettii* Steud. & Hochst., a rather obscure and local mediterranean taxon, to be considered.

The original diagnosis (in Hochstetter 1827) is :

' *Trifolium Biasolettii* Steud. et Hochst. caule parum ramoso radicante adscendente, pedunculis axillaribus petiolisque pilosis, floribus hemisphaerico-capitatis, calycis dentibus subaequalibus, stipulis membranaceis pellucidis, foliolis cuneiformi-cordatis ad medium serrulatis. Bei Pola in Istrien. Steht dem *T. patens* nahe.' (' *T. patens*' is a *lapsus calami* for *T. repens*).

* But flecks are slow to develop at the high temperatures at which the seedlings were grown, and the genetic significance of the ratio of flecked/unflecked phenotypes is uncertain.

This was amplified by Biasoletto (1829), who first noticed the plant, under the superfluous name *T. prostratum* :

' Caulis prostratus radicans, stolonem emittens quandoque abortivum, ad cujus basim pedunculus exiit longior, axillaris, ante inflorescentiam procumbens, postea vero arcuato-erectus, pilosus, pilis patentibus, sub capitulo horizontalibus. Flores hemisphaerico-capitati, amoene rosei. Calycis dentes inaequales, superiores 2 reliquis maiores, virides. Stipulae membranaceae, pellucidae, caulem involventes, arista viridi subulata terminatae. Foliola cuneiformi-cordata ad medium serrulata; petioli ut in pedunculis pilosi. Legumen trispermum. Majo floret. Habitat in graminosis, pascuis siccis'. A number of localities near Pola in Istria are given, including the island Brioni, where Biasoletto first saw it.

Steudel (1841) quotes the name as *T. Biasolettianum* Steud. et Hochst., giving as synonyms *T. repens* L. var. Koch and *T. prostratum* Biasoletto, from which it is quite clear that '*T. patens*' in the original diagnosis should be *T. repens*; all specimens from the neighbourhood of Pola confirm this.

Rouy (1899) describes *T. biasolettianum* Steud. & Hochst. (= *T. Monvernense* Shuttlew. mss.) as ' une forme,' differing from typical *T. repens* in the small size of all its parts; leaflets more deeply obcordate, broader than long and more clearly emarginate; heads almost half as small; calyx teeth more unequal, the upper lanceolate, equalling the tube, the lower triangular, only half as long, more spreading; standard only half as long again as the calyx. The specimen cited in Herb. Rouy was collected by Shuttleworth from slopes in chestnut-groves at la Chartreuse de la Verne near Collobrières, and the general distribution is given as Istria and Dalmatia. Rouy adds that Shuttleworth's specimens are identical with ones from near Pola in Istria. He makes no mention of hairiness or flower colour.

Coste (1901) ignores it, although '*T. Monvernense* Shuttl. n.sp.' was collected as early as 1869 at Collobrières (specimen in Herb. Conservatoire bot. Genève).

Ascherson & Graebner (1908) describe var. B. '*Biasoletti*' [sic], distinguished from *T. repens* var. *repens* by having stems, petioles, peduncles and pedicels pubescent or with spreading setaceous hairs. The stem is described as generally not more than 1 dm. long; leaves with long petioles, leaflets similar to those of *Oxalis acetosella*, obcordate, shortly cuneate at the base, mostly 0·5–1 cm. by 0·5–1 cm., very finely toothed near the apex, often folded up; stipules ovate-lanceolate with a subulate apex, somewhat shining; peduncles long and stiff, generally much longer than the subtending leaf; heads somewhat laxer, usually about 20-flowered; pedicels fairly equal in length; calyx with triangular-lanceolate teeth separated by *obtuse sinuses*, more or less spreading; petals a beautiful pink at first, later darker but not becoming brown, about 5 mm. long, twice as long as the calyx; pod 2–3–seeded, generally not constricted, shortly stalked; seeds oval to almost reniform, red-brown.

They go on to say that it is a very characteristic plant which has been variously assessed, sometimes only as a habitat form of warm localities, sometimes as a species. They think it should be retained as a southern race, the characters not being sufficiently sharp or constant to admit it as a species.

Gams (1924) follows Ascherson & Graebner closely in their description, but gives the name as *T. repens* var. *alpestre* Gussone. This I believe to be incorrect, Gussone's plant (1826) being described as ' glaberrimum ' : it is a dwarf *T. repens* of alpine pastures in the Abruzzi Mountains ' ad nives deliquescentes,' flowering in August and September.

Hayek (1927) gives *T. biasolettii* specific rank, but one of his specimens in Hb. Hayek (Göteborg) is actually *T. physodes* Stev., a species related to *T. fragiferum*, which also has hairy petioles.

Vicioso (1951) also follows Ascherson & Graebner, but omits all reference to hairiness; he quotes a record by Sennen from 2,200–2,300 m. in the Catalonian Pyrenees, but there is no Spanish (or Portuguese) specimen in the Madrid Herbarium.

The specimens I have seen from Provence (Collobrières, Shuttleworth; la Crau, A. Albert; Draguignan, Girod) all have at least slightly hairy petioles and are superficially similar to those from Istria, as Rouy suggested, despite his omission of this character.

Leaf-markings are not evident in any specimens from the herbaria at Kew, Cambridge, Göteborg, Geneva, Toulouse or Madrid, but like flower colour these characters are usually not preserved. Some specimens are less generally hairy than the description of Ascherson & Graebner suggests; these are usually relatively lush plants which may well have come from shaded sites under *Castanea*. Sometimes the petiolar hairs are fulvous, but this may be an artefact.

Both *T. biasolettii* and *T. occidentale* differ from *T. repens* in their hairy petioles and their relatively broader leaflets, and their habitats are generally similar – warm dry places not far from the coast. The published descriptions of *T. biasolettii* would, however, suggest a number of significant differences from *T. occidentale*.

T. biasolettii	*T. occidentale*
Leaflets deeply obcordate.	Leaflets only slightly emarginate.
Stipules membranaceous, pellucid, shining.	Stipules matt, opaque, strongly vinous red.
Calyx-teeth entire, triangular-lanceolate, separated by obtuse sinuses, the two uppermost longer than the rest, ± spreading.	Calyx-teeth ovate-lanceolate, overlapping at the base, the two upper often with one or two prominent denticulations on the upper margin and about twice as long as the two lateral teeth, ± parallel or convergent.
Corolla pink, not becoming brown.	Corolla creamy-white (never pink), becoming pale to dark brown.

In fact, examination of specimens of *T. biasolettii* from Istria and Provence shows that not only are the descriptions frequently misleading but also that other important differences distinguish *T. biasolettii* from *T. occidentale*. Specimens of *T. biasolettii* from Draguignan have most of the leaflets obtuse, and not emarginate or obcordate; the standard is generally 8–10 mm., including claw (presumably Ascherson & Graebner's ' 5 mm.' refers to the limb alone); and I fail to understand their emphasized description of ' obtuse sinuses ' between the calyx teeth.

Figure 3 shows camera lucida drawings of the two upper and two lateral calyx teeth of specimens of *T. occidentale* and typical *T. repens* from Caerthillian Cove, W. Cornwall, and of *T. biasolettii* from the *locus classicus* in Istria and from Draguignan in Provence. The calyces of herbarium material were soaked in water, with a little wetting agent added, for a day before splitting the calyx along the dorsal side, opening it out, and mounting in glycerine jelly. It is evident that the shape of the teeth, triangular-lanceolate, is very similar in *T. repens* and *T. biasolettii*; that the lateral teeth are only a little shorter than the two upper in both *T. repens* and *T. biasolettii* from Istria, but appreciably shorter (relatively) in *T. biasolettii* from Provence (as Rouy's description suggests); and shorter again in *T. occidentale*, in which the ovate-lanceolate teeth, with the two upper convergent, are very distinct from all the rest. The denticulations often present (especially in cultivated plants, or in well grown plants in the field) on the upper calyx-teeth of *T. occidentale* are absent from the calyx illustrated, which was collected in the field in June from a site on very shallow soil.

Further evidence that *T. biasolettii* is more closely related to *T. repens* than to *T. occidentale* comes from examination of leaflets of herbarium material after soaking in water (with a wetting agent) for a day. Leaflets of dried *T. repens* regain the characteristic translucence of their lateral veins with this treatment, and the two leaflets, one from Istria and one from Provence, of herbarium material of *T. biasolettii* examined in this way also show translucent veins, whereas leaflets of dried *T. occidentale* retain their opaque veins after soaking. Although the mesophyll of the leaflets of *T. biasolettii* is somewhat collapsed and decayed in the herbarium material, microtome sections of material both from Istria

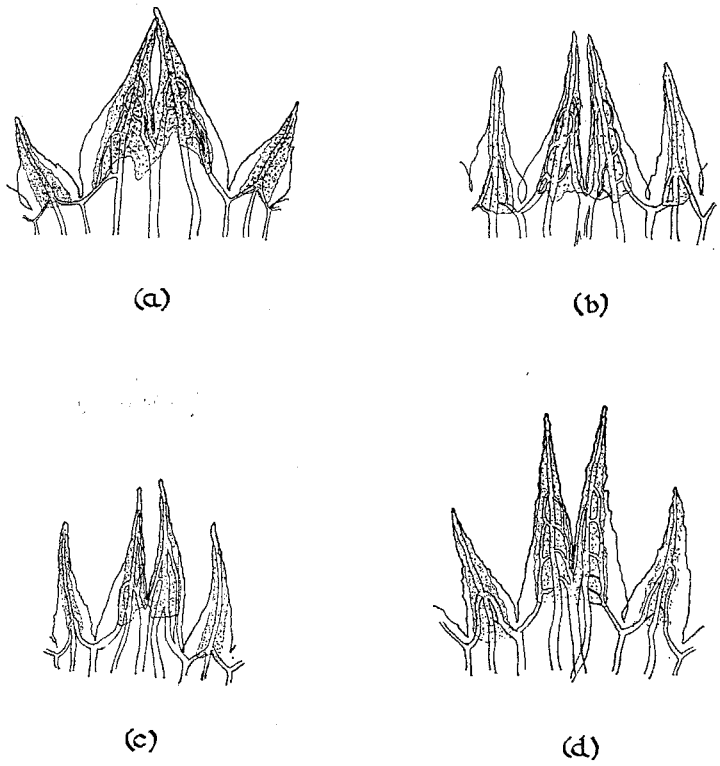

Fig. 3. The two upper (adaxial) and two lateral calyx teeth of (a) *Trifolium occidentale*, Caerthillian Cove; (b) *T. repens*, Caerthillian Cove; (c) *T. biasolettii*, Istria; and (d) *T. biasolettii*, Provence. All from herbarium material soaked in water for a day. Stippled areas : chlorenchyma. Scale : × 10.

and Provence suggest most strongly that their vascular anatomy more closely resemblee *T. repens* in that the mechanical tissue is very well developed above the lateral veins at ths expense of the palisade mesophyll (compare Figure 2). The soaked leaflets of *T. biasolettii* also suggest that the fine teeth on their margin are more numerous (15–30 on each side) than in *T. occidentale* (6–8), and again resemble *T. repens* in this respect. On the other hand, the length/breadth ratios of the soaked leaflets of *T. biasolettii* are nearer to those of *T. occidentale*, but there is clearly a wide variation and a statistical survey cannot be made on the scanty herbarium material available.

We still need more information about *T. biasolettii* from living plants – chromosome number, breeding behaviour and whether the flowers are scented or not – before coming to a firm conclusion about its status, but the morphological evidence leads me to the conclusion that *T. biasolettii* is more closely related to *T. repens*, with which it may well be conspecific, than to *T. occidentale*; and that for the time being *T. occidentale* is best regarded as a distinct species.

Acknowledgments

Among the many friends to whom I am indebted for assistance, advice and discussion are Humphrey Gilbert-Carter who suggested the epithet '*occidentale*,' Professor T. G. Tutin and Dr. S. M. Walters for general discussion on taxonomic problems, Mr. J. P. M. Brenan for helpful comments on the manuscript, Mr. P. D. Sell for advice on typification, Dr. A. L. Peck for assistance with the Latin diagnosis, Dr. H. L. K. Whitehouse for advice on cytology and compatibility, Messrs. M. J. E. Coode and M. J. Swift for the chromosome counts, Mr. P. Freeman for cutting sections and making phenological observations, Mr.

R. L. Jefferies for some soil analyses, Dr. C. D. K. Cook, Mrs. Henning, Mr. and Mrs. R. C. L. Howitt, Miss J. E. Tutin and Mrs. E. W. Woodward for collecting material, the curators of the herbaria at Geneva, Göteborg, Madrid and Toulouse for the loan of specimens, and above all Dr. L. C. Frost with whom most of the field work was done and who has helped in ways too numerous to mention.

References

ASCHERSON, P. & GRAEBNER, P. (1908). *Synopsis der Mitteleuropäischen Flora*, VI. 2 (Lieferung 56), pp. 500–501. Leipzig.

ATWOOD, S. S. (1942). Genetics of pseudo-self-compatibility and its relation to cross-incompatibility in *Trifolium repens*. *J. agric. Res.*, **64**, 699–709.

ATWOOD, S. S. (1944). The behaviour of oppositional alleles in polyploids of *Trifolium repens*. *Proc. Nat. acad. Sci., Wash.*, **30**, 69–79.

BIASOLETTO, B. (1829). Berichte über eine Reise durch Istrien. *Flora*, **12**, 532.

BRAUN-BLANQUET, J. & TÜXEN, R. (1952). Die Pflanzenwelt Irlands. *Veroff. geobot. Inst. Rübel*, **25**, 224–421.

CLAPHAM, A. R., TUTIN, T. G. & WARBURG, E. F. (1952). Flora of the British Isles. Cambridge.

COOMBE, D. E. & FROST, L. C. (1956). The heaths of the Cornish serpentine. *J. Ecol.*, **44**, 226–56.

COSTE, H. (1901). *Flore Descriptive et Illustrée de la France*. **1**, 343. Paris.

DARLINGTON, C. D. & WYLIE, A. P. (1955). *Chromosome Atlas of Flowering Plants*. London.

GAMS, H. (1924). in Hegi, G., *Illustrierte Flora von Mittel-Europa*, IV. 3 (Leguminosae), pp. 1302–1307. München.

GUSSONE, J. (1826). *Plantae Rariores quas in Itinere per oras Jonii ac Adriatici Maris et per Regiones Samnii ac Aprutii*, pp. 307–8. Naples.

HAYEK, A. (1927). Prodromus florae peninsulae Balcanicae. *Repert. nov. Spec. Regn. veg.*, Beih. **30**, Bd. 1, 854.

HENDRYCH, R. (1956). Některé výsledky revise československých jetelů. *Preslia*, **28**, 403–12.

HOCHSTETTER, C. F. (1827). Ueber die Leistungen des botanischen Reisevereins im Jahr 1826. *Flora*, **10**, 72.

PANDEY, K. L. (1957). A self-compatible hybrid from a cross between two self-incompatible species in *Trifolium*. *J. Hered.*, **48**, 278–81.

POORE, M. E. D. (1955). The use of phytosociological methods in ecological investigations. II. The practical issues involved in an attempt to apply the Braun-Blanquet system. *J. Ecol.*, **43**, 245–69.

ROUY, G. (1899). *Flore de France*, **5**, 79. Asnières & Paris.

STEUDEL, E. T. (1841). *Nomenclator Botanicus*, ed. 2, **2**, 705. Stuttgart & Tübingen.

VICIOSO, C. (1952). Tréboles españoles. *An. Jard. bot. Madr.*, **10**, (Año 1951), 347–98.