

The coastal ecodeme of *Parnassia palustris* L.

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ABSTRACT

Cultivation and breeding experiments have shown that *Parnassia palustris* L. var. *condensata* Travis & Wheldon (Parnassiaceae), a coastal ecodeme, retains its characteristic, dwarf, clumped habit and larger ratio of flower diameter to stem height in cultivation, and breeds true from seed. Its taxonomic rank of variety is therefore upheld, and its name is lectotypified by a specimen collected by J. A. Wheldon from W. Lancs., v.c. 60. It has two cytodesmes, with $2n = 18$ and 36 .

MORPHOLOGICAL VARIATION

The existence of a distinctive, coastal ecodeme of *Parnassia palustris* L. in the British Isles had been known for some time (Hall 1839; Wheldon & Wilson 1907; Druce 1911) before it was given taxonomic rank as var. *condensata* (Travis & Wheldon 1912). It was described from "the sand-dunes on the coasts of Lancashire and Cheshire", and was distinguished from var. *palustris* by the following characters: shorter stature; branched rhizome producing more (4-20) and thicker (1.5-1.6 mm in diameter) stems; more tufted basal leaves, the laminae of which are usually as long as or longer than the petioles (rather than shorter); a cauline leaf immersed amongst, or only slightly protruding above the basal leaves (rather than elevated); larger flowers (25-37 mm or more in diameter); and a larger capsule (12-16 mm long). In order to examine these differences, measurements were made of British and Irish specimens of *P. palustris* at BM, CGE, DBN, E, LIV, LTR, NMW, RNG and TCD for the characters listed by Travis & Wheldon (1912). It became clear that these authors underestimated or, in some cases, misjudged the amount of variation to be found within each variety, such that the actual differences between the characters are less clear-cut than they claimed (Table 1), and a distinction between the varieties must be made on the characters considered in combination. For example, variation in stem height and especially in flower diameter is such that any distinction based on these characters individually is either impossible or at best very difficult. However, when the two characters are considered together, the pattern of variation in each variety is different. In var. *palustris* short specimens usually have proportionally smaller flowers, whereas in the dwarf var. *condensata*, the reduction in flower size is much less marked. Thus, when flower diameter is considered as a ratio of stem height, the two varieties can be distinguished much more reliably, and indeed this ratio is probably the best discriminant for use in the field (Table 1).

CULTIVATION AND BREEDING EXPERIMENTS

Cultivation and breeding experiments were conducted to discover whether the coastal ecodeme is merely an environmentally-induced variant (Melvill 1912; Marshall 1913), or whether its features are due directly to genetic factors (Wheldon & Travis 1913). Previous attempts at cultivation have produced different results, partly perhaps because, by general agreement, the species is difficult to grow and maintain in cultivation. Wheldon & Travis (1913) reported that samples of var. *condensata* from S. Lancs., grown by Prof. K. Graebner in Berlin, retained their characteristic features. In contrast, a later but similarly undocumented report stated that var. *condensata* reverted to "average size and habit" after two years in cultivation, becoming indistinguishable from var. *palustris* (Salisbury 1952: 271, 278).

TABLE 1. CHARACTERS USED TO DISTINGUISH VAR. *CONDENSATA* FROM VAR. *PALUSTRIS*
Measurements of wild plants are from herbarium specimens. Measurements of cultivated plants are quoted as means and standard deviations; the statistical tests were applied to these data only.

Character	Wild		Cultivated ^a	
	<i>palustris</i>	<i>condensata</i>	<i>palustris</i>	<i>condensata</i>
Stem height, mm	100–330(–512)	30–150(–230)	186±60	102±66*
Height of cauline leaf above ground, mm	(10–)20–170	5–40	37.5±21.4	30.2±18.0
Basal leaf petiole length: lamina length ratio	(1–)2–6	0.4–3(4)	1.7±0.4	1.9±0.6
Rhizome branched	usually sparingly	usually extensively	usually sparingly	usually extensively
Number of basal leaves ^b	—	—	14±6	28±10*
Number of stems	1–6(–32)	(1–)4–15(–34)	2.0±1.0	3.9±3.2
Stem diameter, mm	0.5–1.5	0.5–2.0	1.3±0.4	1.5±0.5
Flower diameter, mm	15–35	15–35	22.8±4.2	25.0±6.0
Flower diameter: stem height ratio	0.04–0.23	0.15–0.76	0.14±0.04	0.40±0.32**
Capsule length, mm	(6–)9–13	8–15(–20)	9.2±2.3	10.1±1.7

^a Mann-Whitney U-test on cultivated plants:— **significant difference, $P \leq 0.01$; *significant difference, $P \leq 0.05$; all other characters not significantly different. Origins of ramets, sample sizes in parentheses:— Var. *condensata*: Ainsdale, S. Lancs., v.c. 59 (5); Tentsmuir, Fife, v.c. 85 (3); Loch Spiggie, Shetland, v.c. 112 (2). Var. *palustris*: Monks Dale, Derbys., v.c. 57 (3); Malham Tarn, Mid-W. Yorks., v.c. 64 (4); Lochranza, Clyde Is., v.c. 100 (3).

^b Character not used by Travis & Wheldon (1912).

In view of these conflicting reports, I undertook a small cultivation experiment in which transplanted material of both var. *condensata* and var. *palustris* was grown side by side in a glasshouse (Table 1). Ramets taken from plants in the wild were planted in a mixture of 3:1 compost and sand in 7.5 cm plastic pots, and grown in a mist unit; I found this to be the most satisfactory method of maintaining plants in a healthy condition. The duration of cultivation varied, but was usually about 12 months (up to three years in some cases), and the period always included the development of the flowering phenotype from the dormant rhizome.

Three features of var. *condensata* remained distinctive in cultivation: its shorter stems; its larger flower size relative to stem height; and its greater degree of rhizome branching, a character reflected also in the larger number of basal leaves (Table 1). The other differences seen in the field, particularly the position of the cauline leaf and the relative lengths of the petiole and lamina of the basal leaves, tend to disappear in cultivation, with var. *condensata* becoming like var. *palustris*.

Most plants were cultivated for about a year, after which they were pressed, but it is worth noting that the individuals of var. *palustris* from Malham Tarn and of var. *condensata* from Tentsmuir, which were grown for three years, retained their different morphologies as outlined above.

Confirmation that the flower, stem and rhizome differences are under genetic and not environmental control came from a breeding experiment. Self-pollination of cultivated plants of var. *condensata*, collected from Ainsdale, produced full capsules of seeds, showing the plants to be self-compatible. Twelve S_1 seedlings were randomly selected to be raised to maturity. Five of them flowered in their first year, five succumbed to attack by vine weevil and two have remained in a vegetative state. The five flowering plants were all very similar and showed the characteristically large flowers and short stature. The only important difference between the S_1 generation and the parental plants was in the number of stems produced. All S_1 plants had but a single stem, although examination of the rhizomes revealed them to have branched into three or four shoots; these may eventually each produce a flowering stem of their own, thereby generating the clumped appearance typical of var. *condensata*. Seed collected from a wild population of var. *condensata* in Orkney produced similar plants. In contrast, plants of var. *palustris* grown from seed collected in

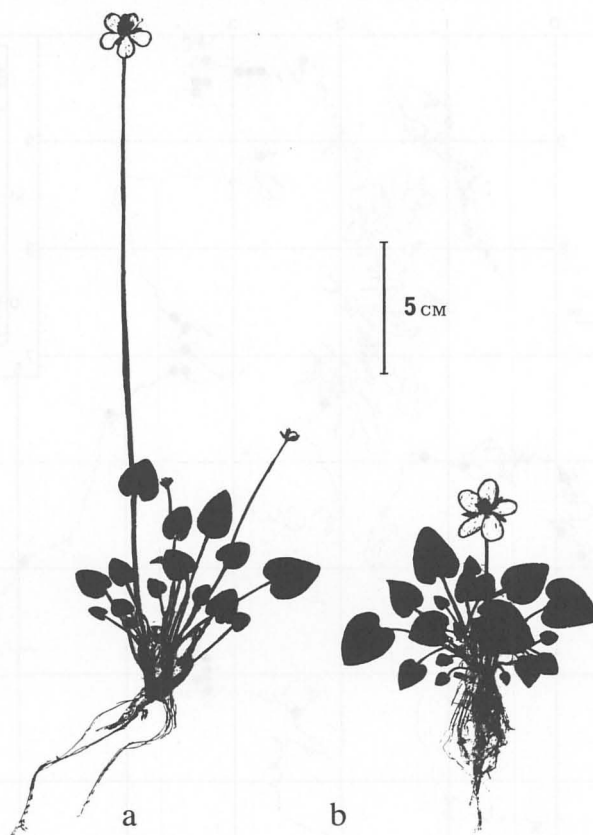


FIGURE 1. Silhouettes of representative specimens of *Parnassia palustris* grown from selfed seed; (a) var. *palustris*, from an Argyll parent; (b) var. *condensata*, from an Ainsdale parent.

Argyll were taller, had smaller flowers relative to stem height, and rhizomes that were less branched (1 (-4) flowering shoots). Representative specimens of both varieties grown from seed are illustrated in Fig. 1.

CONCLUSIONS

The conclusions to be drawn from the herbarium studies and the cultivation and breeding experiments are: i) that *P. palustris* var. *condensata* is a coastal genoecodeme, which constitutes the characteristic variant of the species in machair-type habitats, usually dune-slacks, or in the short turf on the tops of sea-cliffs; and ii) that it is appropriate to award it taxonomic recognition at the rank of variety, because it is a local rather than a consistently regional variant (Du Rietz 1930).

Some comment should be made here on the contrary results obtained by Salisbury (1952) mentioned earlier. It is possible that more than one coastal variant exists, and that Salisbury's material represented an environmentally induced, phenotypic copy of var. *condensata*. Such plastocodemes sometimes occur in coastal populations with an otherwise genetically fixed phenotype (Akeroyd, in press), but how frequent such plants may be in populations of var. *condensata* is unknown.

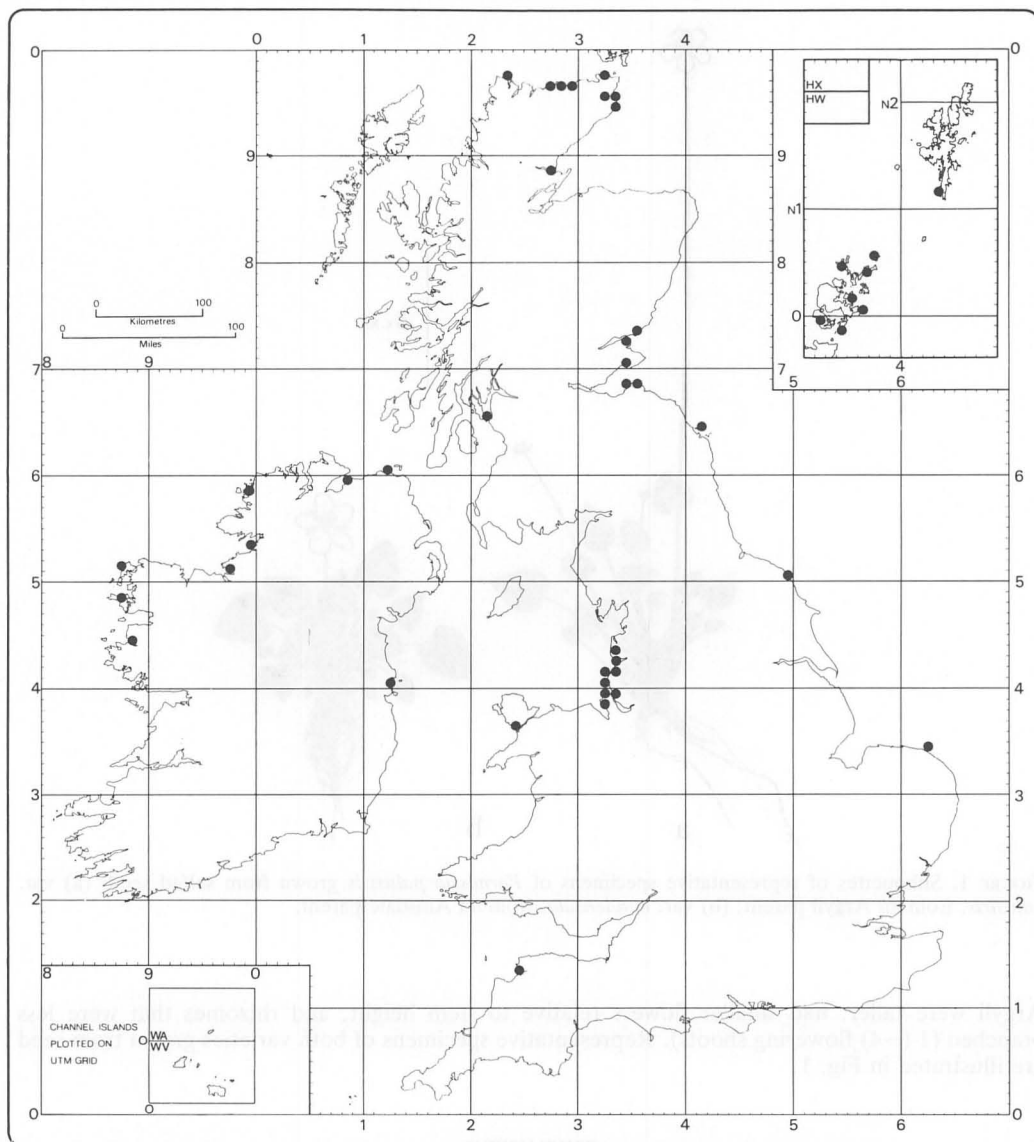


FIGURE 2. Distribution of *Parnassia palustris* var. *condensata* in the British Isles (all records).

TAXONOMIC ACCOUNT

The following description is based entirely on specimens from Great Britain and Ireland.

PARNASSIA PALUSTRIS L. var. *CONDENSATA* Travis & Wheldon in *J. Bot., Lond.*, 50:256 (1912). TYPE: N. of St Annes, [W. Lancs., v.c. 60], Sep. 1900, *J. A. Wheldon* (Lectotype: NMW, designated here).

Rhizome usually much-branched. Stems (1)–4–15(–34), usually less than 15(–23) cm tall, diameter 0.5–2 mm. Basal leaf lamina 8–25 × 7–20 mm, petiole 7–30(–40) mm, usually less than 1.5 times as long as the lamina. Cauline leaf cordate or amplexicaul, rarely deltoid, 5–25(–30) × 3–25 mm,

positioned 5–40 mm from base of stem, the apex of the leaf often level with or below the point to which the apices of the basal leaves reach when positioned alongside the stem. Flowers 15–35 mm in diameter, usually 1/5 or more of stem height; sepals 4–10 × (1–)2–4 mm; petals 6–16 × 5–12 mm, with 7–11 veins; staminode lamina 2–3 mm, longer than broad, narrowed abruptly or tapering to a claw, bearing 7–14 filiform divisions, 2–4 mm long; filaments 3–6 mm; anthers 2–3 mm. Capsule ovoid to globose, obtuse or rounded at the apex, 8–15 (–20) × 9–16 (–21) mm. Chromosome number, $2n = 18, 36$ (Gornall unpublished, based on native material).

There are no Travis or Wheldon specimens predating the protologue in W. G. Travis's herbarium at LIV. Therefore, I have designated the Wheldon specimen from the latter's herbarium at NMW as the lectotype because it is the only one which obviously pre-dates the protologue and is fairly characteristic of the variety. Far better material, collected from Freshfield, S. Lancs., v.c. 59, was widely distributed by Wheldon (1913) as part of a Botanical Exchange Club distribution, but I have been unable to discover whether it was collected before the protologue was published (both are dated August 1912).

DISTRIBUTION

The distribution of var. *condensata* in the British Isles, based on herbarium specimens, is shown in Fig. 2. Records are from the following vice-counties: 4, 27, 52, 58–60, 62, 67, 68, 82, 85, 90, 100, 107–09, 111, 112, H21, H27, H28, H34, H35, H39 and H40. Some populations of *P. palustris* from cliff-tops on the coast of Co. Durham, v.c. 66, are referable to var. *palustris* and grow in a wet meadow habitat, rather than in short turf. Some plants of var. *palustris* from exposed, inland populations (often at high elevations) may resemble var. *condensata* in their dwarf, compact habit, although they usually do not have the characteristically large ratio of flower diameter to stem height. Whether this dwarfness is genetically fixed or not is unknown.

In Europe, var. *condensata* has been collected from dune-slacks in north-western France (Brittany), the Netherlands and Denmark, and, like many coastal ecotypic variants (Akeroyd in press), it appears to be restricted in its occurrence to north-western Europe; southwards and eastwards it grades into var. *palustris*.

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