

Taxonomy, morphology and distribution of *Atriplex* hybrids in the British Isles

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ABSTRACT

A study based on field, culture and experimental work delineates six hybrids in the genus *Atriplex* indigenous to the British Isles. Detailed morphological descriptions are given and distribution maps and illustrations are provided for *A. glabriuscula* Edmondston \times *A. longipes* Drejer; *A. glabriuscula* \times *A. praecox* Hülphers; *A. glabriuscula* \times *A. prostrata* Boucher ex DC.; the variable *A. longipes* \times *A. prostrata* (= *A.* \times *gustafssoniana* Taschereau, **hybr. nov.**, which includes var. *gustafssoniana* and var. *kattgatensis* (Turesson) Taschereau, **comb. et stat. nov.**); *A. littoralis* L. \times *A. prostrata* (= *A.* \times *hulmeana* Taschereau, **hybr. nov.**); and *A. littoralis* \times *A. patula* L. Hybrid derivatives involving *A. longipes*, widespread on the coasts of the British Isles, are responsible for many of the identification problems in the *A. prostrata* group.

INTRODUCTION

Jones (1975a) summarized the literature reports of *Atriplex* hybrids in the British Isles and recorded the presence of seven natural hybrids. As Jones herself noted, however, some of the hybrids reported on the basis of intermediate specimens were doubtful, and as I have explained elsewhere (Taschereau 1986), some of these reports are almost certainly wrong.

Hybrids in *Atriplex* are particularly difficult to recognize without a foundation of experimental work and field studies. One reason for this is the extensive variation, both genetic and phenotypic, exhibited by so many of the species. Genetically distinct morphs, differing in such characters as leaf shape, habit or colour, are known in several species (Taschereau 1985a). Morphological and habit changes occur also in response to environmental factors. This phenotypic plasticity of *Atriplex* has long been recognized as complicating the identification of many species. As long ago as 1860, for example, C. C. Babington wrote that, "*Atriplexes* on fat land are amongst the most undeterminable of plants" (A. M. Babington 1897).

Another complicating factor in *Atriplex* hybrid and species recognition has been the widespread occurrence of hybrid derivatives. Like their facultatively autogamous parents, hybrid derivatives perpetuate themselves by selfing. Unlike many first or second generation hybrids, they are highly fertile, often range well beyond the parent populations, and may occupy an ecological niche different from that of either of the parents. Unaware of their hybrid nature, taxonomists have dealt with these species-like entities in various ways. *Atriplex longipes* \times *prostrata*, for example, has given rise to a number of more or less distinctive morphs, some of which are very widespread. Babington's (1841) *A. rosea* (non L.) is, in part, a derivative of this hybrid (see, for instance, the sheet in E labelled "*A. rosea*, Little Hampton Sussex, 1837 com. L. W. Borrer", in Babington's handwriting and printed "from Charles C. Babington"); Westerlund's (1861) type collection of *A. patula* var. *bracteata* is also a derivative of this hybrid, as is Turesson's (1925) *A. longipes* subsp. *kattgatense*.

Except for *A. laciniata* L., all the *Atriplex* species indigenous to the British Isles are known to hybridize. With the experimental studies of Turesson (1925), Hulme (1957), Gustafsson (1972, 1973a, 1973b, 1976) and my own studies (Taschereau 1985b, 1986), it is possible to distinguish many of the *Atriplex* hybrids in the British flora and to identify most of them with reasonable certainty. This paper describes and illustrates six hybrids and one hybrid variant, gives their distribution, and discusses their taxonomy.

MATERIALS AND METHODS

The field, cultivation and experimental work upon which this study is based have been set forth in detail in Taschereau (1985a, b, 1986). Data from field studies were supplemented by specimens sent to me between 1977 and 1978 by participants in the B.S.B.I. *Atriplex* Survey.

Material from the following herbaria was studied: **ABD, BM, C, CGE, DBN, E, K, LD, LIV** (incl. herb. Barbara Hulme), **LIVU, MANCH, NMW, OXF, S, SLBI, TCD** (abbreviations according to Kent & Allen (1984) and Holmgren *et al.* (1981)). I have annotated the entire holdings of the following herbaria: **ABD, CGE, DBN, E, LIV, LIVU, TCD**. Also, approximately half of the large holdings of **NMW** have been annotated by me.

My collections, including those of the B.S.B.I. Survey, are deposited in **MANCH**, except for type specimens as indicated in the text. A duplicate set of Gustafsson's (1976) hybrid collections used for reference is in my possession (**herb. Taschereau**). Each dot on the distribution maps of the hybrids is supported by one or more specimens filed in **MANCH**.

ATRIPLEX LONGIPES: A KEY TAXON

The occurrence of *A. longipes* in the flora of the British Isles was confirmed only in 1977, although its presence was earlier suspected (Hulme in Aellen 1964; Jones 1975b). Taschereau (1985b) indicated that *A. longipes* is the key to understanding much of the confusing variation within the *A. prostrata* group. *Atriplex longipes* hybridizes with *A. prostrata* and with *A. glabriuscula*, species that only rarely hybridize with each other. The hybrid derivatives involving *A. longipes* are widely distributed on the coasts of the British Isles and occur also in inland salt marshes. They are usually highly fertile and often species-like in their behaviour. Morphologically, they may resemble one or the other parent, or be distinct from either parent. They may occur in the same habitat as one or the other parent species, or occupy a different ecological niche. This situation, and some of the frequent identification problems it has given rise to, are summarized in Fig. 1.

Many of the long-recognized taxonomic problems in the *A. prostrata* group in Britain have been caused by the presence of hybrid derivatives involving *A. longipes*. There yet remains, however, a residue of plants, especially from the northern and north-western coasts of Scotland and the coasts of Shetland, which have not been satisfactorily identified except to group.

DESCRIPTIONS

1. *A. glabriuscula* Edmondston × *A. longipes* Drejer (Fig. 2)

Most plants resembling *A. glabriuscula* in habit and general morphology. Prostrate or ascending. Lower leaves triangular, or rhombic to ovate-lanceolate; base cuneate, obtuse or truncate. Bracteoles rhombic or ovate-lanceolate, herbaceous at the apex, frequently large (10–20 mm long) and foliose, some of the axillary ones stalked, margins united almost up to the middle or only near the base, thickened towards the base by a moderately to strongly developed silvery brown spongy tissue, dorsal surface often strongly reticulate-veined in the lower part.

Habitat and Distribution. Exposed coastal beaches, frequently with *A. glabriuscula*. Hybrid derivatives between *A. glabriuscula* and *A. longipes* are frequent on the coasts of northern Scotland and north-western England. Reported by Gustafsson (1976) as rare in western Scandinavia with one record from Bodö, Norway. The distribution in the British Isles is shown in Fig. 3.

Variation and Biosystematics. Hybrid derivatives, although often occurring in the same habitat as *A. glabriuscula*, are well-established and independent of the parent taxa. The hybrid was artificially synthesized by Gustafsson (1973a). Seed germination of F₁ artificial hybrids was only between 10% and 30%, although the pollen stainability of F₂ plants was between 80% and 100% (Gustafsson 1973a).

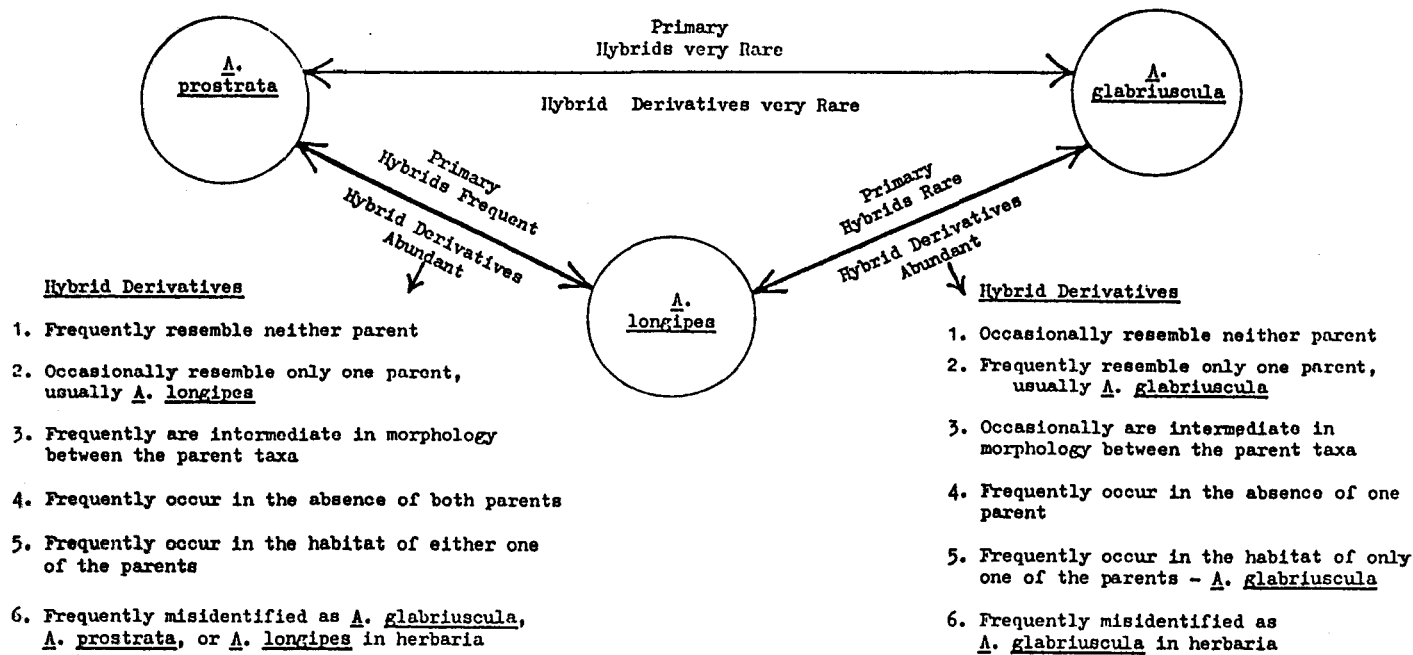


FIGURE 1. Hybrid derivatives involving *A. longipes*.



FIGURE 2. *A. glabriuscula* × *A. longipes*.

The name *A. glabriuscula* f. *pedicellata* Abromeit has been applied to variants of this hybrid with large stalked bracteoles (Aellen 1960; Gustafsson 1976).

Diagnostic Characters. The hybrid is most frequently confused with *A. glabriuscula*, from which it can be distinguished by the stalks present on some of the bracteoles in the leaf axils, and the tendency of many bracteoles to develop large foliose tips and thickened, veiny basal portions.

2. *A. glabriuscula* Edmonston × *A. praecox* Hülphers (Fig. 4)

Most plants resembling *A. praecox* in leaf outline but similar to *A. glabriuscula* in bracteole morphology. Prostrate-spreading or ascending. Foliage mostly reddish or less commonly green, resembling *A. praecox*. Lower leaves lanceolate-triangular or ovate-lanceolate; base cuneate to

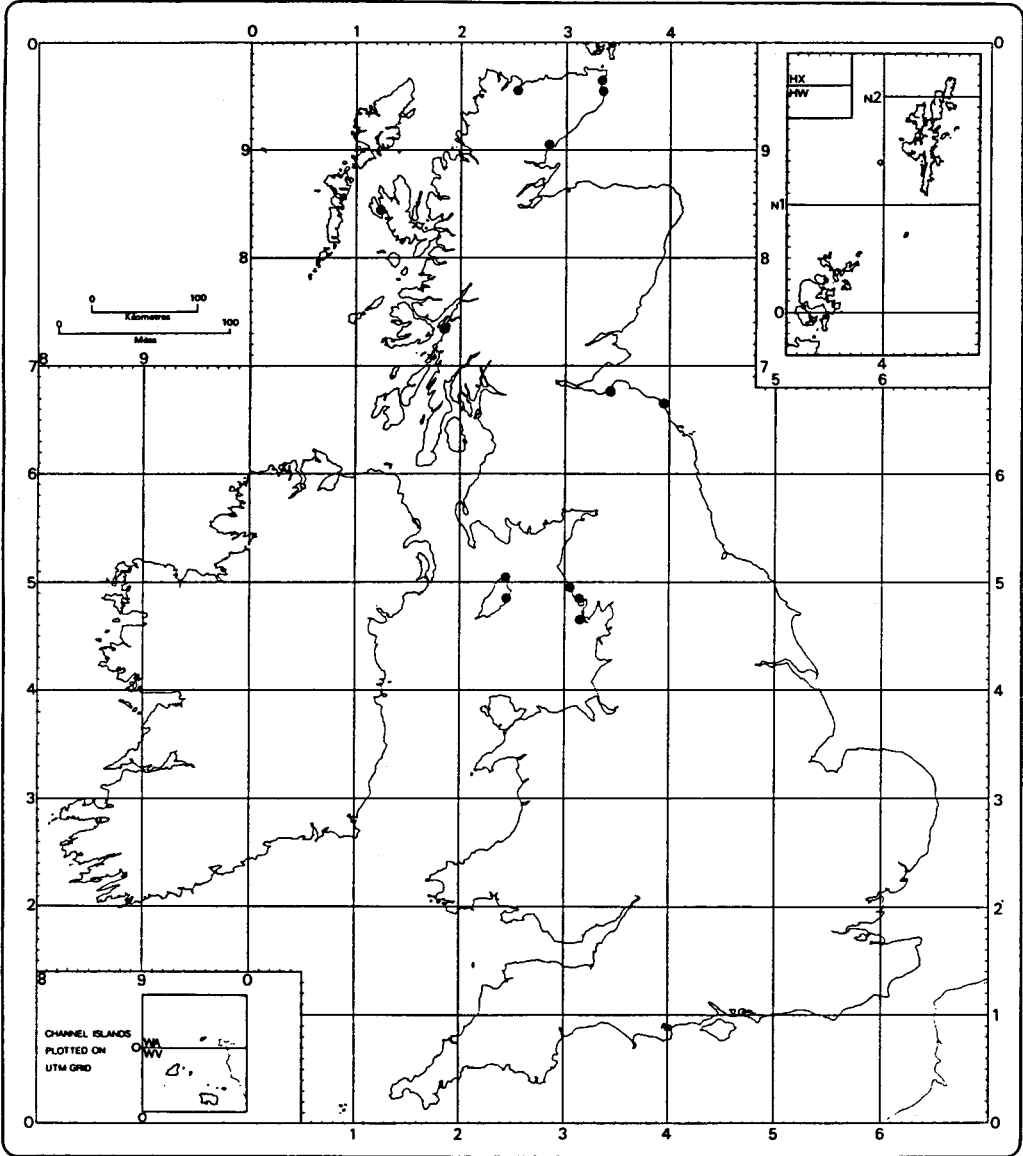


FIGURE 3. Distribution of *A. glabriuscula* × *A. longipes* in the British Isles.

obtuse. Upper leaves lanceolate to linear. Bracteoles rhombic, sessile or slightly stalked (stalks c. 0.5 mm long), margins united almost up to the middle, thick-spongy towards the base, dorsal surface smooth and without prominent veins.

Habitat and Distribution. Very rare in north-western Scotland and Shetland where it occurs with *A. praecox* and *A. glabriuscula* at the margins of protected sea inlets. Reported by Gustafsson (1976) as rare in the northernmost parts of Norway. The distribution in the British Isles is shown in Fig. 5.

Variation and Biosystematics. The hybrid was artificially synthesized by Gustafsson (1973a). In the artificial hybrids, pollen fertility and seed germination were greatly reduced. In two crosses, one had

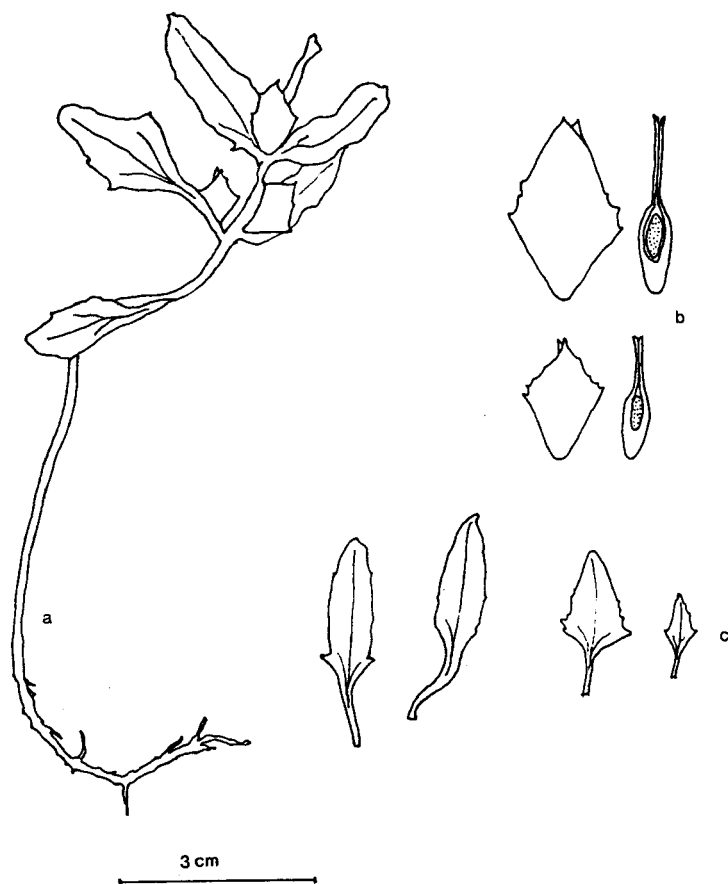


FIGURE 4. *A. glabriuscula* × *A. praecox*. a) Habit, b) Bracteoles (not to scale), c) Leaf variation.

73% and the other 67% stainable pollen, and only 40% to 50% of the seeds germinated (Gustafsson 1973a).

Diagnostic Characters. The small, often reddish, leaves resembling those of *A. praecox*, in combination with the thick-spongy bracteole characteristic of *A. glabriuscula*, will distinguish this hybrid.

3. *A. glabriuscula* Edmondston × *A. prostrata* Boucher ex DC. (Fig. 6)

Plants generally intermediate in morphology between the parent species; ascending. Lower leaves triangular as in the parents; base subcordate, truncate to obtuse. Inflorescence spiciform as in *A. prostrata*. Bracteoles sessile, smaller than *A. glabriuscula* and in more densely packed glomerules, thick-spongy, margins united almost up to the middle, dorsal surface bi-tuberculate or smooth, without prominent veins. Seeds mostly less than 3.0 mm wide, radicle variously positioned and directed.

Habitat and Distribution. Middle beach zone on coastal beaches with the parent species. Rare from southern England in v.c. 15 (Badmin 1978) to south-western Scotland in v.c. 74 and on the eastern

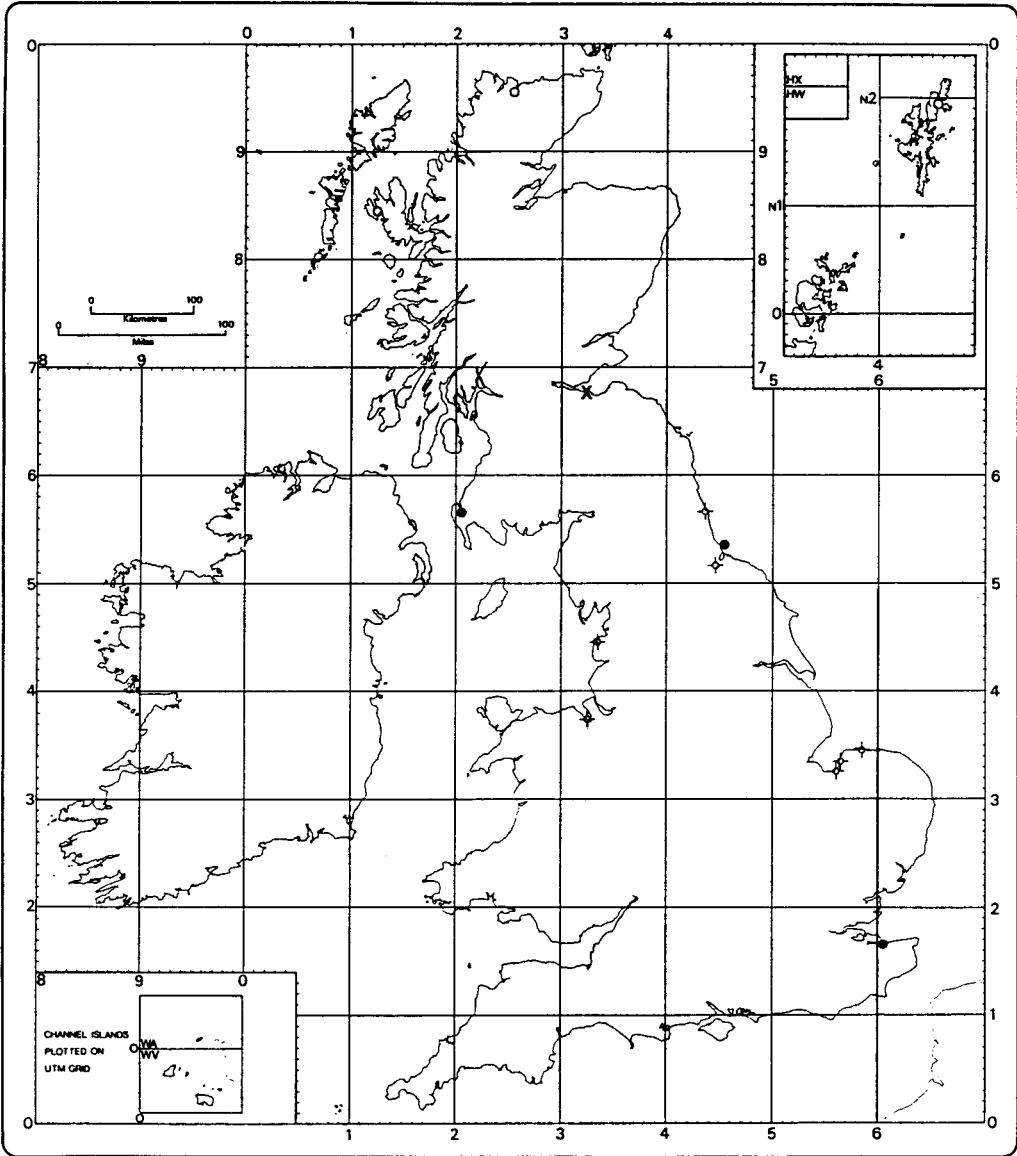


FIGURE 5. Distribution of *Atriplex* hybrids in the British Isles: ○ *A. glabriuscula* × *A. praecox*; ● *A. glabriuscula* × *A. prostrata*; ⊙ *A. littoralis* × *A. prostrata*; × *A. littoralis* × *A. patula*.

coast of England in v.c. 66. Reported by Gustafsson (1976) as relatively rare in the western parts of Scandinavia. The distribution in the British Isles is shown in Fig. 5.

Variation and Biosystematics. The hybrid was artificially synthesized by Gustafsson (1973a). Most of the artificial hybrids had a high pollen stainability (four out of seven crosses had greater than 90% stainable grains), but seed germination was poor. Seeds from two of the crosses did not germinate and in the other seven crosses seed germination varied between 1% and 40% (Gustafsson 1973a).



FIGURE 6. *A. glabriuscula* × *A. prostrata*. a) Habit, b) Bracteoles and seed.

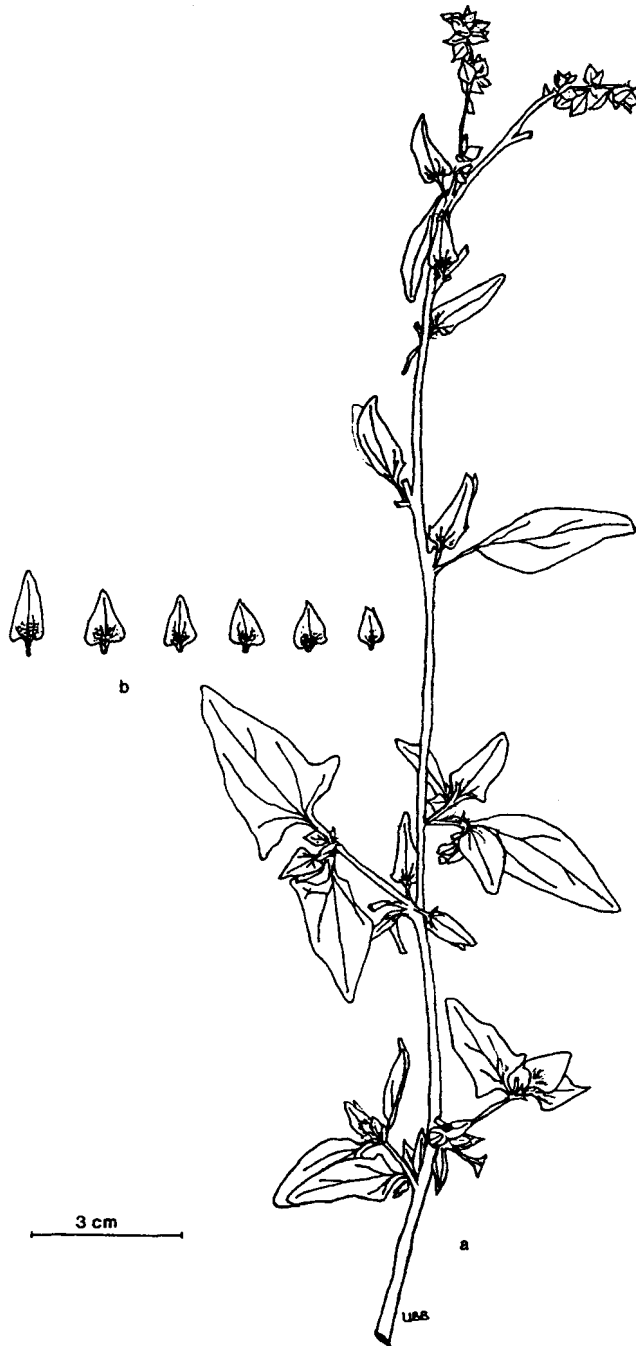


FIGURE 7. *A. x gustafssoniana* var. *gustafssoniana*. a) Habit, b) Variation in bracteoles.

Germination of seeds from spontaneous hybrids in nature was also low (less than 40%) (Gustafsson 1973b).

From identified material in herbaria, it is clear that hybrid derivatives of *A. longipes* × *A. prostrata* and *A. longipes* × *A. glabriuscula* have occasionally been mistaken for *A. glabriuscula* × *A. prostrata*. This hybrid is rare; it is not common as suggested by Moss & Wilmott (1914) and by Jones (1975a), and earlier records should be re-examined.

Diagnostic Characters. The size, morphology and arrangement of the bracteoles are most useful in distinguishing the hybrid from its parents: the bracteoles are thick-spongy and frequently bituberculate as in *A. glabriuscula*, but generally much smaller and arranged in somewhat dense, leafless, spiciform inflorescences similar to those of *A. prostrata*.

4. *Atriplex* × *gustafssoniana* Taschereau, *hybr. nov.*

HOLOTYPE: Snettisham, N. W. Norfolk, v.c. 28. Margin of *Phragmites australis* stand in open area of saltmarsh by the coast, 18 September 1976, *Taschereau & Libbey* 76–12 (DAO).

Hybrida ex *A. longipes* Drejer et *A. prostrata* Boucher ex DC. orta. Folia inferiora elongato-triangularia vel ovato-lanceolata, basi truncata vel cuneata. Quidam bracteoli in axillo foliorum superiorum magni, tenuiter herbacei, petiolati, angulis lateralibus acutis saepe bene evolutis, superficie plusminusve forte reticulo-venata basin versus.

i) var. *gustafssoniana* (Fig. 7)

Atriplex patula var. *bracteata* Westerlund, *Sveriges Atriplices* 57 (1861). **LECTOTYPE:** Sweden, Skåne; sheet labelled “*Atriplex patula* Lin. – *bracteata* Wester., Skåne, C.A.W.” (S); chosen by Taschereau in *Watsonia* 15: 204 (1985).

Erect, ascending or prostrate, with long-spreading lower branches. Lower leaves elongate-triangular in erect forms, or ovate-lanceolate in some prostrate forms, usually much longer than wide (length/width ratio 1.5–2.5); base cuneate to truncate. Bracteoles 4–9 mm long, triangular, sessile or stalked but usually some with stalks 0.5–5.0 mm long present in the axils of the upper leaves and branches; thin-herbaceous, sometimes becoming foliose; margins united at the base, lateral angles pointed and often strongly developed; dorsal surface often strongly reticulate-veined toward the base.

Habitat and Distribution. Coastal sand and shingle beaches, often remote from the parent species. In coastal, estuarine and inland salt marshes, frequently in stands of *Agropyron pungens* or *Juncus maritimus* and at the margins of *Phragmites australis* stands. One of the commonest *Atriplex* taxa on the coasts and in estuaries around the British Isles and occasional in inland saltmarsh vegetation at Nantwich, Cheshire and Preesall, Lancashire. Reported by Gustafsson (1976) as common on the western coast of Sweden northwards to the southern parts of Norway, and as relatively rare in Denmark and the Baltic area. Most of the *Atriplex* populations along the Swedish western coast investigated by Gustafsson (1973b) included individuals of hybrid origin. The distribution in the British Isles is shown in Fig. 8.

Variation and Biosystematics. The cultivated progeny of most wild *A. longipes* × *A. prostrata* derivatives exhibited a mixture of parental characters. Many plants, however, showed a degree of segregation that gave some indication of their parentage (Taschereau 1986). In the artificial hybrids (Gustafsson 1973a) pollen stainability was high (16 of 22 crosses had greater than 80% stainable pollen grains), but seed germination was greatly reduced. Germination varied from 0% to 60% but in 20 out of 23 crosses less than 30% germinated. In the wild hybrids examined by Gustafsson (1973b) both pollen fertility and seed germination were reduced. The F₁ hybrids in many of the artificial crosses were morphologically similar to *A. prostrata* even when *A. longipes* was used as the female parent (Gustafsson 1973a). A similar situation has been observed in wild British plants (Taschereau 1985b). In parts of Scandinavia where grazing has disturbed the habitat, introgressive hybridization between *A. longipes* and *A. prostrata* has given rise to a more or less continual gene

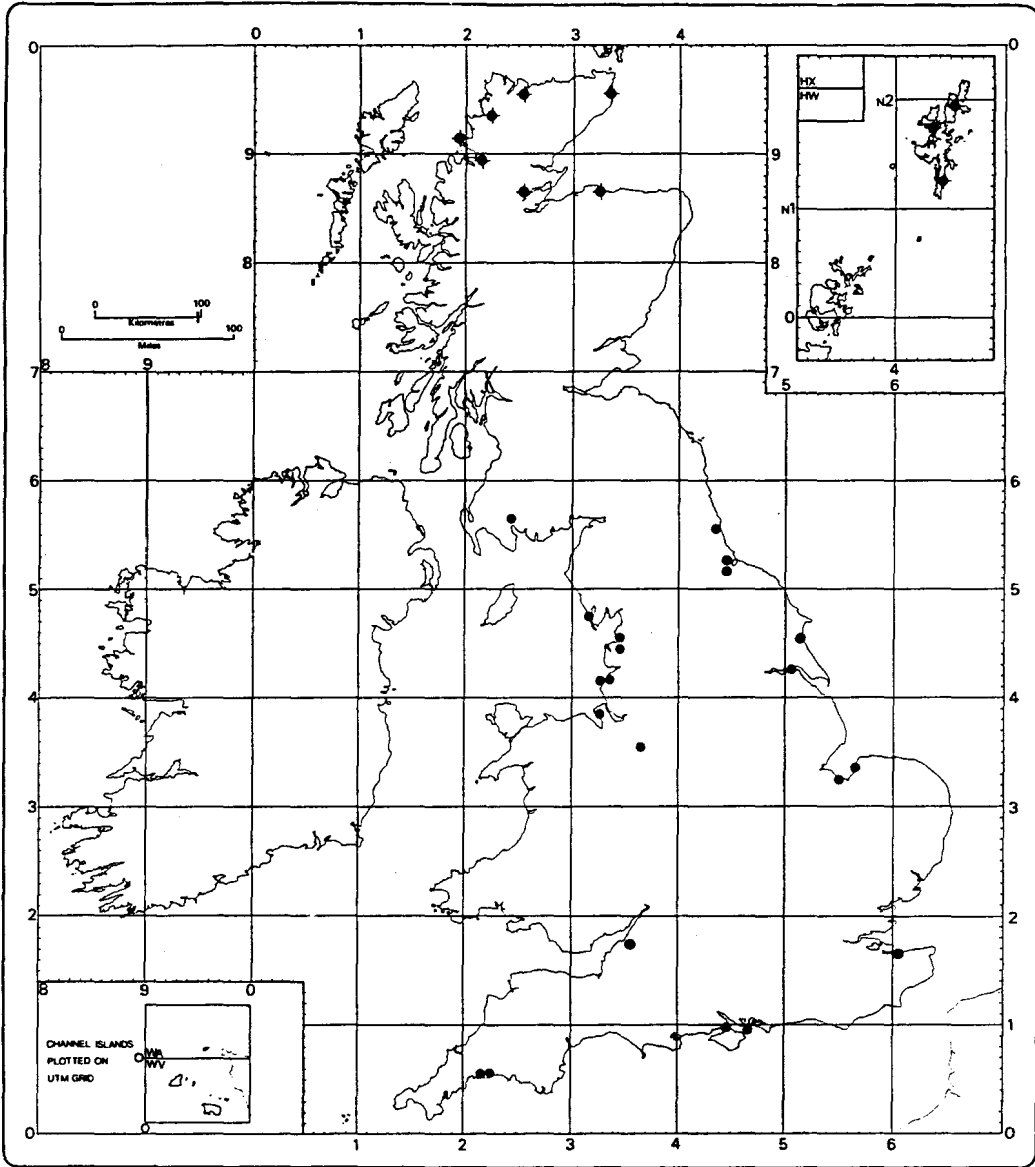


FIGURE 8. Distribution of *A. × gustafssoniana* in the British Isles: ● var. *gustafssoniana*, ●◐ var. *kattegatensis*.

flow between these species (Gustafsson 1974). This seems to be the situation in most parts of Britain where, according to Adam (1978), undisturbed estuarine salt marsh vegetation (the habitat of *A. longipes*) is virtually non-existent.

Hybrid derivatives are well established and independent of the parent species. They are extremely variable and almost every combination of parental characters has been observed in the field. On the basis of size, habit and habitat our plants can be broadly placed into two groups: 1) Salt marsh variants. Large ± succulent plants, erect, spreading to straggling, up to 1 m high; stems strongly angled; leaves large, elongate-triangular, with cuneate to truncate base; occurring in tall salt marsh vegetation or at the margins of such communities. 2) Beach variants. Small non-succulent

or more or less succulent plants, prostrate, decumbent or weakly erect; lower branches wide-spreading and often longer than the central axis; angularity of stems variable; occurring on \pm exposed coastal beaches and at the margins of or in sparsely covered or open areas of coastal salt marsh vegetation.

Diagnostic Characters. In the axils of some of the upper leaves occur large thin-herbaceous, stalked bracteoles with lateral angles pointed and often strongly developed and the dorsal surface more or less strongly reticulate-veined toward the base. The occurrence of these characteristic bracteoles in combination with elongate-triangular or ovate-lanceolate lower leaves at least some of which have a more or less truncate base is diagnostic of this hybrid.

Nomenclatural Note. The type specimen of *Atriplex patula* var. *bracteata* Westerlund is a hybrid derivative between *A. longipes* and *A. prostrata*. Plants such as this are part of the myriad of beach variants comprising the hybrid derivatives described here under var. *gustafssoniana*. While I have myself seen specimens along the Swedish coast at Malmö that are similar to the type, the characters distinguishing such plants are, in my view, not constant enough to merit further formal taxonomic recognition. In addition, there has been considerable confusion regarding the application of the name var. *bracteata* Westerlund since Aellen (1960) applied it (as f. *bracteata*) to plants of *A. patula* L. s.s. with foliose bracteoles (ennatia), and Fernald (1950) applied the name *A. patula* var. *bracteata* to plants described as very similar to typical *A. patula* "but with fruiting bracts 1–1.5 cm long" occurring on marshes of Cape Breton, Nova Scotia. Fernald's specimen from Cape Breton (GH!) representing his var. *bracteata* is, like Westerlund's type, a hybrid derivative in the *A. prostrata* group. Furthermore, Westerlund's (1861) description is not sufficiently detailed to exclude certain variants of *A. patula* sens. str., and his statement, "Hab. rara ad vias circa Lund et in litore marino ad Malmö Scaniae" would seem to include the ruderal *A. patula* ("ad vias circa Lund"), along with the obligate halophytic derivatives of *A. longipes* \times *A. prostrata* ("in litore marino ad Malmö Scaniae").

ii) var. *kattgatensis* (Turesson) Taschereau, **comb. et stat. nov.** (Fig. 9)

A. longipes subsp. *kattgatense* Turesson in *Lunds Univ. Arsskr.*, N.F. Adv. 2, 24 (4): 4 (1925). LECTOTYPE: Sweden, Bohuslan, Tanums socken, Otteron, August 1880, *H. Thedenius* (S); the specimen annotated "*A. longipes* kattgatense Turess. nov. subsp.", to the middle-left, chosen by Gustafsson in *Opera Botanica* 39: 29, 31 (1976).

Plants 10–30 cm, prostrate to decumbent, spreading with the lower branches longer than the central axis. Stems sub-angular, striate, green and stramineous striped or reddish. Branches opposite to sub-opposite in the lower region of the central axis but often barely separated by extremely short internodes. Foliage bluish-green, frequently reddish, succulent; mature lower and upper leaves glabrous; juvenile leaves glabrous above, sparsely farinose on the undersurface. Lower leaves 2.0–3.5 cm long, 1.0–2.5 cm wide, with a pair of outpointing to forward-curving basal lobes; margins irregularly serrate or entire; apex acute; base cuneate. Upper leaves smaller, linear-lanceolate, without or with basal lobes; margins entire or weakly toothed. Inflorescence axillary to the base of the plant and shortly terminal, leafy to the tip. Bracteoles 3.5–5.0 mm long, at least some shortly stalked (stalks 0.5–1.0 mm long), rhombic to triangular-lanceolate or ovate-lanceolate; apex acute or acuminate; base cuneate; margins entire, united at the base or somewhat higher up to the lateral angles; lateral angles pointed or rounded, not strongly developed; mostly herbaceous and thin but sometimes slightly thickened toward the base by the presence of spongy tissue; dorsal surface smooth or with a few short, weak appendages; venation obscure or somewhat prominent towards the base. Seeds polymorphic, black or brown, orbicular, 1.5–2.5 mm wide; radicle sub-basal, obliquely up-pointing.

Habit and Distribution. Exposed coastal beaches close to the salt water where the vegetation is very sparse; often with *A. praecox* on the shores of somewhat less exposed sea inlets. Frequent in northern Scotland and occasional in Shetland. Reported by Gustafsson (1973b) as common on the western coast of Sweden. The distribution in the British Isles is shown in Fig. 8.



FIGURE 9. *A. × gustafssoniana* var. *kattegatensis*. a) Habit, b) Bracteoles and seed.

Variation and Biosystematics. Gustafsson's (1973b) experimental work with this taxon indicates it is probably a more or less well established product of hybrid origin. Some of the cultivated offspring of var. *kattegatensis* raised by Gustafsson (1973b) from seeds collected in nature showed considerable morphological variation. He observed segregates similar to *A. longipes* and to *A. prostrata* as well as intermediate forms. Some offspring, however, did not differ from the parent and showed no indication of segregation. Likewise, plants cultivated from var. *kattegatensis* collected at Ullapool, v.c. 105, did not segregate (Taschereau 1986). These non-segregating forms may represent ancient

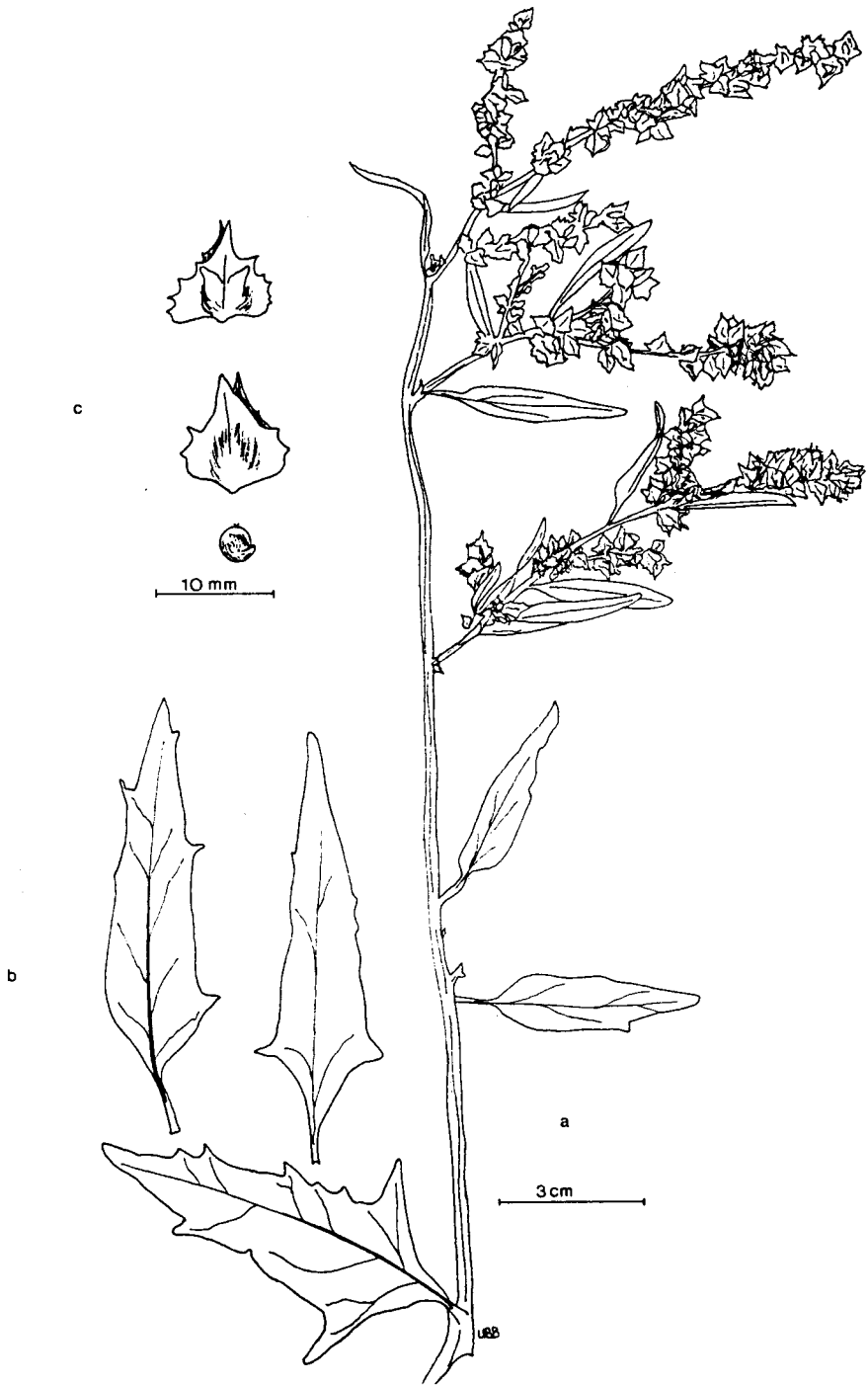


FIGURE 10. *A. x hulmeana*. a) Habit, b) Leaf variation, c) Bracteoles and seed.

or historical hybrids that have arisen by stabilization of an F_2 or later segregant adapted to the specialized exposed habitat that is colonized by neither of the parents. In the British Isles, var. *kattegatensis* appears to have primarily a northern distribution and specimens from southern regions such as those from v.c. 15 (Badmin 1978) require further study.

Hybrids. None have been identified from nature. Gustafsson (1973b) has made experimental hybrids between var. *kattegatensis* and *A. longipes*, *A. praecox* and *A. prostrata*. Pollen fertility in the majority of crosses was greater than 80% but hybrids with reduced fertility were common. Morphological variation in the F_1 and F_2 progenies of the experimental hybrids was considerable and difficult to categorize because of the free recombination of morphological characters that occurred.

5. *Atriplex* × *hulmeana* Taschereau, *hybr. nov.* (Fig. 10)

HOLOTYPE: Wolferton, Norfolk, England, 18 September 1976, *Taschereau & Libbey* 76–24 (DAO).

Hybrida ex *Atriplex littoralis* L. et *A. prostrata* Boucher ex DC. orta. Folia primaria succulenta, triangulari-lanceolata, cum lobis basalibus patentibus vel falcatis, basi cuneata. Bracteolae triangulares vel ovati-triangulares, crassae, spongiosae, basibus conjunctae.

The hybrid is named after Barbara Hulme, British botanist and first person to produce experimental hybrids in *Atriplex* by controlled crossing (Hulme 1957, 1958). Her elegant work provided an experimental basis for understanding the relationship of *A. patula* to *A. littoralis* and to members of the *Hastata* complex (*A. prostrata* group) in Britain.

Erect, very robust plants with thick stems and ascending branches. Foliage dark green, glabrous, very succulent. Lower leaves triangular-lanceolate with a pair of strongly developed out-pointing to forward-curving basal lobes; length at least twice the width; margins irregularly sinuate-dentate, attenuate to the apex; base strongly cuneate. Upper leaves lanceolate, without basal lobes or with a single lobe developing on one side only, entire or with few teeth. Bracteoles 5–10 mm long, sessile, broadly triangular to ovate-triangular; apex acute; base truncate to cuneate; margins denticulate or with only a few teeth, united at the base; lateral angles rounded and weakly developed; thick-spongy; dorsal surface strongly bi-tuberculate or smooth; venation obscure. About 70–80% of the bracteoles contain well-developed seed. Both large-brown and small-black seed types are frequent in the same plant. Segregants showing a wide range of character combinations sometimes occur amongst the F_1 plants described above. Many of the segregants are largely sterile and often weak-stemmed, but some are vegetatively very vigorous and develop into quite prominent plants. The following three variants appeared in cultivation and are sufficiently common in the field to be mentioned.

1. *Patula*-leaf variant. Plants with leaves like *A. patula* that possess the falcate basal lobes so characteristic of this species.
2. *Serrata*-leaf variant. Plants with markedly sinuate-dentate leaves like extremes of plants formerly called *A. littoralis* var. *serrata*.
3. *Gigas* variant. Plants up to 1 m high with thick stems and gigantic leaves with ovate-lanceolate irregularly lobed lamina up to 15 cm long and 4 cm wide.

Habitat and Distribution. Disturbed habitats where the parent species are present in abundance: disturbed banks of estuaries recently dredged, earthen sea walls less than three years old, salt marshes disturbed by rabbit grazing. Occasional on the eastern and western coasts of England in v.cc. 28, 58, 60, 66. Jones (1975a) states it has been recorded as rare in Denmark. The distribution in the British Isles is shown in Fig. 5.

Variation and Biosystematics. See Taschereau (1986) for a detailed discussion. Jones' (1975a) report of the putative hybrid *A. glabriuscula* Edmondston × *A. littoralis* L. probably refers to *A.* × *hulmeana* as discussed in Taschereau (1986).

Diagnostic Characters. The characteristic shape of the large succulent lower leaves in combination with the spongy-thick bracteoles is diagnostic of this hybrid.



FIGURE 11. *A. littoralis* × *A. patula*.

6. *Atriplex littoralis* L. × *A. patula* L. (Fig. 11)

Erect, up to 0.5 m high. Lower leaves up to about 6 cm long and 3 cm wide, ovate-lanceolate to rhombic with a pair of forward-curving basal lobes; succulent, glabrous, dark glossy-green; margins irregularly serrate to sinuate-dentate; base strongly cuneate. Upper leaves smaller, similar to the lower ones or lanceolate to linear with or without basal lobes, entire or with a few teeth. Bracteoles rhombic, sessile; margins denticulate, united up to the middle; thick-spongy, tuberculate; occurring

in dense terminal inflorescences. The majority of bracteoles are empty and collapsed. Dispersed between these sterile bracteoles, however, are occasional larger, well-formed, filled out bracteoles that contain seed. From one to five of the larger fertile bracteoles occur in the inflorescences of most branches.

Habitat and Distribution. Disturbed weedy ground by the coast where both the parents are growing together. Known only from one locality in Scotland at Leith Docks, Edinburgh, v.c. 83. Reported by Turesson (1925) from Lomma and Torekov along Öre Sund in south-western Sweden. The distribution in the British Isles is shown in Fig. 5.

Variation and Biosystematics. This hybrid has been experimentally synthesized three times: by Turesson (1925), by Hulme (1957) and by Taschereau (1986), but its occurrence in nature is very rare. It has been looked for on numerous occasions in locations where the parents were growing together but found only once. A published record from Findhorn, v.c. 95, Scotland (Webster 1979) is a mistake. Subsequent to publication of this record, I changed my original identification of the hybrid specimen to *A. littoralis* × *A. prostrata*. For a detailed discussion of the biosystematics see Taschereau (1986).

Diagnostic Characters. The green, densely spiciform inflorescence consists mainly of small empty uniform bracteoles, but on almost every inflorescence branch, scattered among the green sterile bracteoles, one or two large grey-black seed-containing bracteoles stand out. The plants resemble *A. littoralis* in habit, but the lower leaves are similar to those of *A. patula*. The bracteoles are spongy-thick as in *A. littoralis* but united almost to the middle as in *A. patula*. In early November, the bright dark green colour of the hybrids makes them stand out strongly from the surrounding vegetation. The parent species by this time are mostly brown and dying.

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