THE TAXONOMY OF *POLYGONUM AVICULARE* AND ITS ALLIES IN BRITAIN

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ABSTRACT

The taxonomic history of *Polygonum* species in the section *Polygonum* (*Avicularia*) relating to the British flora is outlined. The merits of the various morphological characters used by authors to separate taxa in previous treatments is discussed. Evidence is produced, supported by results of biometrical, ecological and cytological studies, that the British and W. European forms of the weedy *Polygonum aviculare, sensu lato* comprise four species and a reclassification of these is proposed. Problems in the related British species in the group are discussed and clarified. A key to the British species is included.

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1. HISTORICAL INTRODUCTION

As the nomenclatural problem encountered in the taxonomy of *P. aviculare, sensu lato* is complicated and confused, a more detailed historical taxonomic sketch than usual of the species concerned is necessary for a full understanding of the problem as it exists today. This however includes only the barest detail relevant to the species described.

Linnaeus (1753) includes *P. aviculare* in a division of the genus :

'**Polygonum* foliis indivisis, floribus octandris.'

As the other sections are given names by him, e.g. *Persicaria, Helxine, Bistorta*, it seems clear that he intended *Polygonum* as the sectional name for this group. In it he includes the following species: *P. aviculare, P. erectum, P. articulatum* and *P. divaricatum.* Of these *P. aviculare* is the best known, the commonest and also one which stands first in the group. It is therefore proposed to make *P. aviculare* the type species of the genus and *Polygonum* should be regarded as the name of the section according to the *International Code of Botanical Nomenclature* (1956), replacing later names.

The section was named *Centinode* by De Candolle (1815) with a brief description which was later amplified by Meisner (1826) who called it *Avicularia.*

None of the characters given separate this section sharply from others in the genus. However, there should be little difficulty in recognizing species belonging to it; the axillary flowers alone are a sufficient guide. There is a tendency for certain of the species, e.g. *P. arenarium* Waldst. & Kit. and *P. ramosissimum* Michx., to have the flowers aggregated at the upper nodes only of the leafless branches, forming long spike-like racemes. The fruit characters of these species are however similar to those of the more typical species of this section.

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Polygonum aviculare, sensu lato

Linnaeus (1753) used the binomial *P. aviculare* and gives the following very brief description :

'*Polygonum* floribus octandris trigynis axillaribus, foliis lanceolatis, caule procumbente herbaceo.'

This is an extremely broad description of the plant and would include all the species of the section. The closely related *P. maritimum* appears in the group headed '*Persicaria* pistillo bifidis,' but the diagnosis is :

'*Polygonum* floribus pentandris trigynis axillaribus, foliis lanceolatis, caule stipulis obtecto fruticoso.'

Linnaeus also gives 4 varieties to *P. aviculare*, which are impossible to relate to any species which have been subsequently described in the aggregate.

The first 'species' to be separated from *P. aviculare* L. was *P. littorale*. The original place of publication of this binomial is often wrongly cited. H. F. Link (in Schrader 1800) states in a letter written while on a journey to Portugal that he has seen a variety of *P. aviculare* which is similar to *P. maritimum*, and which has thick juicy leaves and the branches covered wholly with sheaths. This note of Link's does not however contain any name but some authors have referred to it as being the place where *P. littorale* was first published.

The first publication of the epithet *littorale* is in fact by Persoon (1805) when he gives **P. littorale*† with the following description,

'foliis crassis succulentis, caule minus ramoso.'

He cites Link's original plant in Schrader.

Link (1821) later described *P. littorale* with:

Caule procumbente suffruticoso, foliis oblongis acutis venosis carnosis, vaginis ciliatis internodiis multo brevioribus. Hab. in Europae maritimis.

Caulis suffrutescens angulatus. Foliis petiolo brevissimo lamina 10 " 5 " acuta. Cor. alba. Vulgo pro *P. maritimo* colitur at hujus vaginae internodiis aequilia. A. *P. aviculari* differt foliis latioribus magis carnosis, caule suffruticoso.'

From this one learns that the main differences between *P. littorale* and *P. aviculare* are slight, as it is said to differ in only the broader fleshy leaves and the woody or shrubby stem. *P. maritimum* differs in having ochreae as long as or longer than the internodes.

Since this time the plant has sometimes been given the status of a species, sometimes as subspecies or as a variety. Koch (1837) reduces it to that of a variety of *P. aviculare* whereas Meisner (1826) gives it the status of full species.

It is difficult to visualize the kind of plant which Persoon first described and its origin is not quoted in the diagnosis. Many authors of later works have included it under *P. maritimum*. Lindman (1896) contends that Persoon may have in fact described a form of *P. maritimum*.

Babington (1922), Lindman (1912), Moss (1914) and Rechinger (1958) follow Koch in retaining the plant as a maritime variety of *P. aviculare*. Tutin (1952) retains it as a 'microspecies' in the *Polygonum aviculare* aggregate distinguished by characters of the fruit.

It is interesting to note that in the last five years A. & D. Löve (1956 a, & b), Chrtek (1956), Scholz (1959) and Pauvels (1959) do not mention this plant, and its status as a species may be taken as doubtful (see later).

I have made exhaustive attempts to trace the type specimen of *P. littorale* on the Continent. Unfortunately, Persoon's herbarium is apparently lost and almost all Links' specimens at the Berlin-Dahlem Herbarium, including the *Polygonaceae*, were destroyed during the last war. A specimen named by Koch *P. aviculare* var. *littorale* has been seen from the Rijksherbarium, Leiden (L), which fits *P. aviculare*, *sensu stricto*. The specimen exhibited the characteristic fleshiness of the leaves and stems associated with plants growing under halophytic conditions. It seems necessary, therefore, to treat *P. littorale* as a *nomen dubium*.

†Species given by Persoon with an asterisk appear to him to be uncertain or obscure

An investigation of British maritime forms in *P. aviculare sensu lato* has shown that no plants answering to the description of *P. littorale* Pers. exist in this country. A number of herbarium specimens labelled under this name exhibited great morphological differences and were a mixture of either *P. aviculare, sensu stricto*, or *P. arenastrum*. Living plants of the group collected by myself had rather fleshy, glaucous stems and leaves, but these phenotypic differences did not persist in cultivation.

Persoon (1805) also named plants collected by Thiébaud in the *P. aviculare* group as **P. monspeliense* with the following description :

' P. erecta, foliis ellipticis crenulatis, caule erecto stipulis scariosis incisis. Hab. Monspelii; Thiébaud. Distincta species videtur.'

Many later authors in floras have cited Thiébaud as the authority for the name but this is incorrect. It is the earliest name for the taxon *P. aviculare, sensu stricto* (*P. heterophyllum* Lindm.) if the Linnean name is rejected for any reason (see p. 205). I have obtained a photograph from the De Candolle Herbarium at Geneva (**G–DC**) of *P. monspeliense* collected by Thiébaud, and it is typical of plants which I today call *P. aviculare, sensu stricto*. This name will be considered later.

Besser (1822) described a species that he collected in ' Volhynia and Podolia ' (now the Ukraine, Russia), which he called *Polygonum neglectum*. He gives the following description :

' P. floribus 7 octandris, trigynis, subspicatis, foliis lanceolatis, ochreis laceris, internodiis brevioribus, caulibus diffusis patentibus ramosis mihi.'

There have been several different interpretations of this description and it has been the centre of much confusion. Although the plant has never been listed as a member of the British flora, a discussion of its taxonomy is relevant from the point of view of nomenclature.

Besser does not describe the fruit of the plant he collected and later authors describe it differently. Ledebour (1850) gives *P. neglectum* as a synonym of *P. arenarium* Waldst. & Kit., whilst Meisner (1856) includes it *pro parte* under this species and *pro parte* under his own *P. aviculare* var. *angustissimum*. Boreau (1857), on the other hand, suggests that it might be an earlier name for Jordan's *P. rurivagum*.

Several of the more recent treatments of the variation in this group have included *P. neglectum* as a full species. Notable examples of these are Komarov (1936), Lembke (1948), A. & D. Löve (1956) and Scholz (1959). Whilst A. & D. Löve record the plant as being common in Canada, the other three authors are all concerned with its occurrence in eastern Europe. This species will be discussed later.

The Russian botanists Meyer & Bunge (in Ledebour (1824)) first described *P. oxyspermum* from the island of Ösel in the Baltic. Their description is :

' Foliis lineari-lanceolatis subeveniis, floralibus diminutis, ochreis laceris internodiis brevioribus, caule ramoso, ramis erecto-patulis, corollae laciniis apice concavis patulo-conniventibus, semine acuminato corollam superante.'

P. oxyspermum is kept as a species by Meisner in De Candolle (1856), and is placed in the herbaceous section with *P. aviculare*, whereas the very closely related *P. raii* is placed in the suffruticose section with *P. maritimum*. The name appears in several of the older east-European Floras. A plant was named *P. acadiense* by Fernald (1914) as an endemic in N. America but Ostenfeld (in Fernald (1916)) states that after examining Danish and Scandinavian material labelled as *P. raii* he discovered that many of the plants referred to this were in fact *P. acadiense*. He found it to be widely distributed along the coasts of the Baltic and gives records for Denmark, Sweden, Gulf of Riga and arctic Norway. True *P. raii* is according to him confined to the channel coasts (England and France) and neighbouring areas.

Samuelsson (1931) identified *P. acadiense* as conspecific with *P. oxyspermum* after examining the type of Meyer & Bunge in Leningrad. *P. oxyspermum* was recorded in Great Britain during the last century and will be discussed later.

A ' species ' of a most dubious nature, *P. robertii* was described by Loiseleur-Deslongchamps (1827). Specimens were gathered by a M. Robert from a locality near Toulon, France and sent to Loiseleur for determination. The description is :

' Planta caulibus herbaceis procumbentibus diffusis, foliis ovato-lanceolatis virentibus, stipulis membranaceis acutis, floribus 2–3 axillaribus pedunculatis.'

No indication is given of the character of the fruit, but from Rouy (1910) one gathers that the main differences between this plant and *P. aviculare* are to be found here. In *P. robertii* the fruits are small and shining, and the plant is said to be a biennial or perennial. This species is of interest to British botanists in that the name has been frequently quoted as a synonym of *P. raii* Bab. and has been taken by some to be the correct name for this species. C. E. Britton, however, commenting on a specimen gathered from the Killiney Sands, Co. Dublin (v.c. H21) and labelled *P. raii* Bab. 1920, mentions : ' The two names are not synonymous. *P. robertii* is a plant of the Mediterranean area apparently not reaching the British shores, and distinguished by its biennial or perennial root. The achenes are much smaller than in *P. raii* and polished almost as much as *P. maritimum.*'

Babington (1836) described *P. raii** as a new species from plants sent to him from Marazion Bay, Cornwall, as follows :

' Caule procumbente herbaceo, ochreis 2-partitis ovatis demum laceris venis paucis distantibus simplicibus, floribus axillaribus, caryopside laevissima perianthio longiore.'

He was considerably confused about the existence of *P. robertii* and mentions in a letter to W. J. Hooker ' *P. robertii* appears to be a plant that is quite unknown to all botanists except its author and I am quite unable to state whether it is the same as my *P. raii.*'

No authentic material of *P. robertii* could be traced in France. Specimens in the Herbarium, Laboratoire de Phanérogamie, Paris (**P**) labelled as such were not *P. raii* but maritime forms of *P. aviculare, sensu lato.*

However, Reynier (1905) states ' Mutel, ayant examiné dans l'herbier de Robert la plante authentique, la décrit variation à tiges herbacées moins dures du *P. maritimum.*' Lindman (1904) mentions that a specimen of this ' species ' in the State Museum, Stockholm, labelled *P. robertii* Loiseleur, Toulon, ' belongs decidedly to *P. aviculare s.s.*' I feel sure that M. Robert's plant was merely a form of *P. aviculare* with rather more shining fruits than normal.

As no authentic specimens of this species are extant this name must be treated as a *nomen dubium.*

Boreau (1857), incorporating the researches of Jordan, threw the problem of nomenclature in the *P. aviculare* aggregate into even greater confusion by adding five new names and elevating other varietal names to specific status. The four binomials of Jordan (previously unpublished) are *P. agrestinum, P. humifusum, P. microspermum* and *P. rurivagum,* whilst Boreau himself described *P. arenastrum* as a new species as well as *P. polycnemiforme* (Lecoq & Lamotte) Bor. based on *P. aviculare* var. *polycnemiforme* Lecoq & Lamotte, and *P. denudatum* (Desv.) Bor. based on *P. aviculare* var. *denudatum* Desv.

Two of the binomials given by Boreau are relevant to the work on the British plants. These are *P. rurivagum* Jord. and *P. arenastrum* Bor. The relevant parts of his description are given here for purposes of typification.

' *P. rurivagum* Jord. ex Bor. Tige de 1 à 5 dec. grêle, flexueuse, dressée . . . . à nervures saillantes, gaînes brun-rougeâtres. . . . fruit brun mat, un peu luisant, finement chagriné, trigone, à faces excavées, ovoïde, aigu au sommet . . . Champs sablonneux après la moisson.'

' *P. arenastrum* Bor. Tiges très rameuses à rameaux longs étalées, sur le sol, tous très garnis de feuilles rapprochées, petites, ovales ou ovales oblongues, gaînes courtes. . . . fruit brun châtáin, assez luisant, court, terminé en pointe. Sables, graviers etc.'

**P. rayi* or *raji* are mistaken orthographies adopted by many Continental, Scandinavian and American botanists, but no employed by Babington in his original diagnosis

These two names have been taken up as being the correct ones for taxa in the British flora.

Lange (1880) after a botanical expedition to Greenland described a new variety *P. aviculare* var. *boreale* which was later elevated by Small (1895) to specific rank. Lange's original description is as follows :—

'Foliis petiolatis, ½–1 pollicaribus, elliptico-obovatis, obtusiusculis; glomerulis 2–5 floris, floribus pedicellatis, pedicello fere perigonii longitudine; ochreis latis, acutis v. obtusiusculis, apice fissis.' North America, Siberia, Iceland, Faeroes.

Druce in this country was much puzzled by populations which he encountered from the Shetland Islands, subsequently called by him (1922) *P. aviculare* var. *grandiflora*, and this led me to an investigation of the plants of this group occurring in these islands. A number of populations have been obtained from the Shetlands and most of these on investigation have been found to form a distinct taxon. The plants agree with Lange's type collection in the petiolate leaves and in the large fruit and persistent perianth. They have also been compared with gatherings from Iceland, Greenland and Northern Scandinavia. It is regarded here as a distinct species, *P. boreale*, new to the British Isles.

An effort to produce a more satisfactory taxonomic treatment for the species occurring in Europe was attempted by Lindman (1904, 1912). He studied the plants over a greater area of their range than any previous workers and made the group the object of special investigation to which many more recent authors have referred.

He divides the group into three species, *P. calcatum* Lindm., *P. heterophyllum* Lindm. and *P. aequale* Lindm., with a number of varieties. He first separated *P. calcatum* (1904) and later (1912) published the other names in dividing up the forms remaining under *P. aviculare*. It is regrettable, however, that the differences between *P. calcatum* and *P. aequale* are not clear from his description. Lindman states furthermore, that *P. calcatum* is as common in Scandinavia as *P. aviculare*, (including *P. aequale*). The relevant features of Lindman's description of *P. calcatum* are :

'Annual, prostrate, leaves tending to be small elliptical, ovate or obovate. . . Peianth united to the middle, compressed, tubular; segments pale green edged with white. Stamens 5. Nut small 2–2½ mm long, broadly ovate-lanceolate, gradually narrowing at the tip, compressed trigonous, the sides convex, smooth.

Those of *P. aequale* are :

'Annual, stem erect or prostrate, leaves of main stem and flowering branches equal or differing in size, all commonly the same shape. . . Perianth segments equalling the length of the fused base or twice as long. . . Persistent perianth as long as the fruit or a little shorter. Fruit trigonous *c.* 2–3 mm long, ovate or lanceolate, black.'

Lindman's other species, *P. heterophyllum*, is a more satisfactory entity, and is distinguished from the others by the heterophyllous nature of the leaves and by the fruit which is larger, generally up to 3 mm, with three dull, concave sides. Lindman gives five varieties of the latter with the name *rurivagum* as one of them. Hybrids between all species of the group are said to occur. It is presumed that Lindman used new binomials for these taxa on the grounds that the Linnean *Polygonum aviculare* is a *nomen ambiguum*, but nowhere in the literature does he state this.

Moss (1914) follows Lindman very closely in his extensive treatment of the group in Britain but raises *P. rurivagum* to full specific rank.

Tutin (1952) in our most recent Flora treats the Linnean *P. aviculare* as an 'aggregate species' and includes the following as segregates, *P. aviculare* L., *sensu stricto* (= *P. heterophyllum* Lindm.), *P. littorale* Link, *P. rurivagum* Jord., *P. aequale* Lindm., *P. calcatum* Lindm. His account is based on that of Moss (1914) but less detail of the morphology and distribution of the plants in Britain is given.

The four latest studies by specialists on the taxonomy of this difficult group have all appeared since this present work was begun in 1956. The conclusions of these workers differ to some extent among themselves and from my own. There is, however, some measure of agreement over such issues as the number of taxa into which the variation pattern of

P. aviculare in the wide sense can be divided if allowance is made for the areas in which these taxonomists have worked. There is, however, still great confusion and difficulty over the question of the correct binomials which are to be used in naming these taxa. Every effort has been made to discuss the more difficult problems with them. These discussions have helped in reaching the conclusions included in this present treatment, which I believe to be the correct ones.

A. & D. Löve (1956) have worked on Canadian plants and base their reasons for the delimitation of taxa mainly on cytological evidence. They give little detail of the morphology of the species they include and this has made exact comparisons with them and the British taxa difficult in most cases. These authors retain *P. heterophyllum* Lindm., *P. aviculare* L. (= *P. aequale* Lindm.) and *P. rurivagum* Jord. (!). They include also *P. neglectum* Bess. and state that it ' has been introduced, and is common in Canada.' *P. calcatum* Lindm. is reduced to a subspecies of *P. aviculare* L. *P. boreale* is treated as a subsp. *boreale* of *P. heterophyllum.* No reason is given by A. & D. Löve for equating *P. aequale* Lindm. with *P. aviculare* L.

The interest of the work by A. & D. Löve lies in the fact that they are the first workers in this field to attempt a complete correlation of cytological observations with morphological differences in these plants. Their work, however, contains several counts of chromosome numbers which are not consistent with those made on the same taxa in this country. A discussion of these differences will appear later.

The treatments of Chrtek (1956) and Scholz (1958–59) may be considered jointly since they have both worked in eastern Europe. Although the rank of the taxa they propose is considerably different and a new binomial is introduced their results are similar. Chrtek proposes four groups at the level of subspecies. These are subsp. *monspeliense* Pers., subsp. *rectum* Chrtek, subsp. *calcatum* (Lindm.) Thell. (new to Czechoslovakia) and subsp. *aviculare* (= *aequale* Lindm.). The name subsp. *rectum* is a new one to the already long list of names in the aggregate, and Scholz (1959) elevates it to specific rank in his treatment* and keeps the taxa above as full species together with *P. neglectum.*

The value of Chrtek and Scholz's work is difficult to assess since they each seem to have worked in a vacuum and have referred to existing literature rather than specimens on which to base their conclusions. Types have been entirely neglected.

Pauvels (1959) has been able to establish the existence of two separable taxa in *P. aviculare, sensu lato* in the Belgian flora. He contends that plants gathered from different localities in Belgium fall easily into two groups, *P. aviculare* L., *sensu stricto*, and *P. aequale* Lindm. which are both extremely variable.

2. Analysis of taxonomic characters

(a) *Vegetative Characters*

Habit.

The habit and size of the plant have been frequently used in the past as diagnostic for a particular species, (Boreau 1857, Ascherson & Graebner 1913, Chrtek 1956). Habit varies with the age of the plant and is a most variable feature depending on environmental conditions, and I consider it to be of little taxonomic significance.

Ochreae.

The hyaline outgrowths at the nodes which characterize the family *Polygonaceae* are of only limited use as taxonomic criteria in the *P. aviculare* aggregate. The ochreae of *P. rurivagum* are however longer than those of the other species recognized.

Ochrea-length and the type and number of veins are, on the other hand, highly significant characters in the separation of *P. raii* and *P. maritimum*; those of *P. maritimum* are frequently as long as the upper internodes, and silvery in colour, with 8–12 branched

*He drops this name later (1960) in a key to the species in this group.

veins. Those of *P. raii* are shorter; the mean length of a population from Hayling Island, S. Hants (v.c. 11), was 0·6 cm, with up to a maximum of 6 unbranched veins.

Leaf size and shape: Heterophylly

The leaves are all simple and entire from 0·3 cm to 5·5 cm in length, and 0·1 cm to 1·8 cm wide, varying in shape from very narrowly lanceolate, to oblong-lanceolate and ovate-spathulate. The petiole is evident only in *P. boreale* where it is longer than, and protrudes beyond, the enveloping ochrea. Stress has been laid on leaf-characters by previous workers, and they are frequently the only ones mentioned in their keys, (e.g. Boreau 1857). Because of the caducous nature of the foliage, leaf characters must be used with caution, and in this work they have always been related to other more stable features such as fruit-size and length of the fruiting perianth.

Two characters were used for biometrical data :

1. A linear measurement of the length and breadth of the largest stem leaf. The length was measured from the point of insertion of the leaf, including the petiole if present, to the apex. The width was taken at the broadest part of the leaf.

2. The index of heterophylly for each plant in any given sample was obtained by dividing the length of the main stem leaf obtained in 1 by the length of the lowest leaf of the branch subtended by this stem leaf.

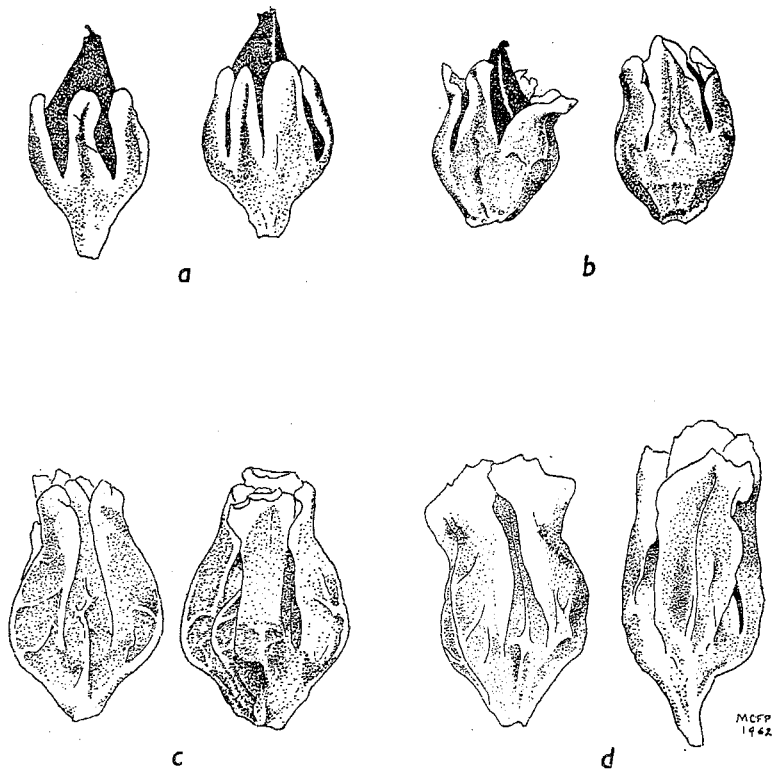


Fig. 1. Camera lucida drawings of fruiting perianths of *Polygonum* spp., × 8.
(a) *P. rurivagum*, Devil's Dyke, Cambs. (b) *P. arenastrum*, Chedworth, Glos.
(c) *P. aviculare*, Brill, Bucks. (d) *P. boreale*, nr. Scalloway, Shetland Is.

(b) *Flower and Fruit Characters*

It is very probable that the small size of the flowers and fruits and their insignificant position in the axils of the leaves is a reason for their having been neglected as taxonomic criteria by many earlier authors. The very striking differences between the fruits of *P. maritimum* and *P. aviculare* are not mentioned by Linnaeus. The flowers of the *Polygonaceae* are monochlamydeous. In the species in this section there are 5 (rarely 4 or 6) perianth segments which vary in length according to the species. The perianth segments have a green midrib and a red, pink or greenish-white petaloid border. The width of this border varies, being greater in the two littoral species *P. raii* and *P. maritimum*, and in *P. boreale*, than in the other species. Colour-differences between the species have been given as diagnostic by many authors in the past, but the present study has revealed that there is no correlation between colour and the different species.

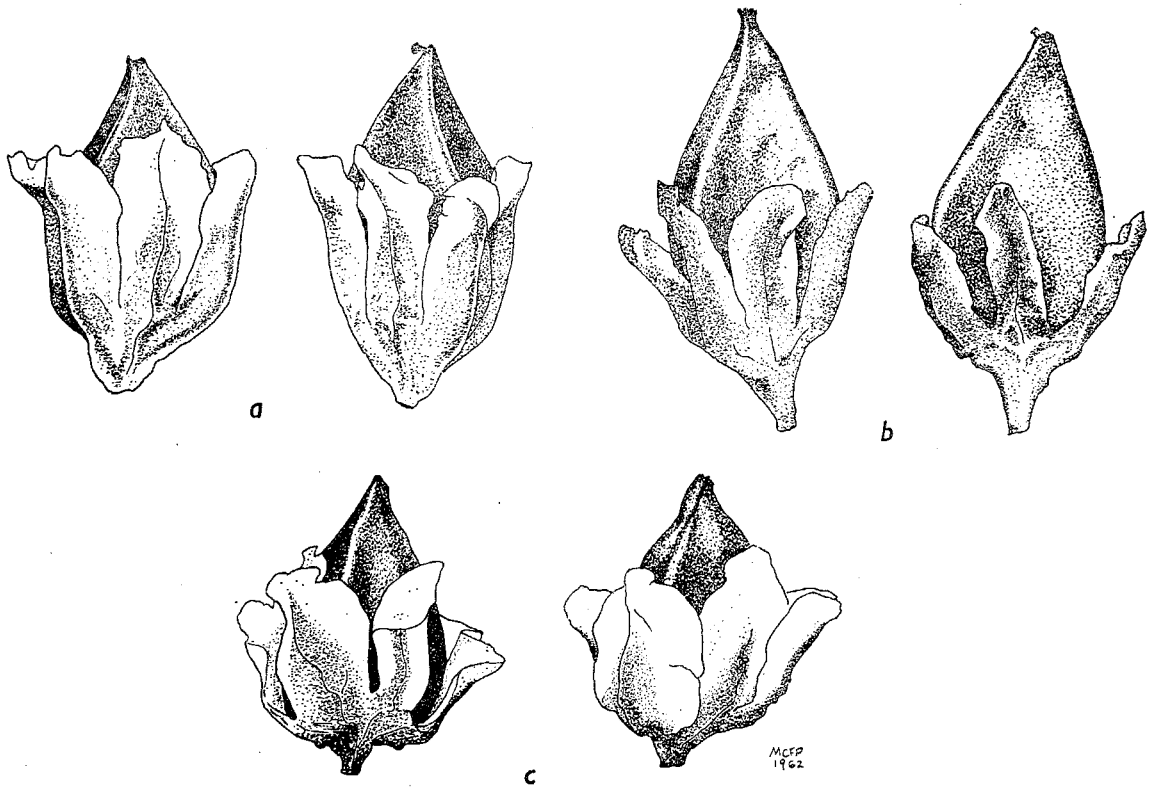


Fig. 2. Camera lucida drawings of fruiting perianths of *Polygonum* spp., × 8.
(a) *P. raii*, Hayling I., S. Hants., (b) *P. oxyspermum*, Irevik, Gotland, Sweden.
(c) *P. maritimum*, Herm, Channel Is.

The perianth is persistent and encloses the fruit forming an enveloping cover. It is dispersed with it when mature. The length of the fruiting perianth segments shows a considerable amount of variation. In some species the perianth is divided almost completely to the base of the flower so that there is practically no tube, whereas in others it is less deeply divided. The tube is then longer, sometimes three quarters of the total perianth length. The length of the persistent perianth, the length of its fused portion and the length of the perianth segments have been found to be diagnostic. (See Fig. 1 & 2). The following

parameters were measured using a low-power binocular microscope with a × 10 eye-piece containing a calibrated micrometer scale and a × 3·4 objective.

3. Length of the persistent perianth.
4. Length of the perianth segments, obtained by subtracting the length of the joined portion of perianth from the total perianth length.
5. The ratio $\frac{\text{Total perianth length}}{\text{Perianth segment length}}$

Stamen number

Lindman (1912) states that *P. heterophyllum* has generally eight stamens, five in an outer whorl and three in an inner, whereas *P. aequale* has five, a whorl of three and another of two. Three typical populations were analysed in detail for this character. There is wide variation in the number of stamens in the flowers of any one plant in all three species (Table 1). Stamen number seems to vary with the age of the flower in the inflorescence. Also flowers developed late in the year were found on the whole to have a lower number than earlier formed ones.

TABLE 1.
Percentage frequency of stamen number in flowers of 3 different species.

Species	*Number of stamens*						*Total No. of flowers*	*No. of plants*
	4	5	6	7	8	9		
P. aviculare, sensu stricto	1·26	1·95	7·36	27·8	59·6	1·95	163	52
P. arenastrum	2·82	42·4	8·02	11·26	35·4	0	148	48
P. rurivagum	0	2·58	7·22	20·6	68·0	1·03	194	50

Fruit

The fruit develops from a tricarpellary ovary to form a nut which is usually three-sided. It may be examined by removing the persistent perianth with a sharp scalpel. Absolute length of the fruit has been used by many botanists to segregate species in the past, as in *P. microspermum* for very small fruited specimens, and *P. heterophyllum* (= *P. aviculare* L., *sensu stricto*) with large fruit. On the whole the longer fruits tend to be broader, so that fruit-size offers a supplementary character to that of fruit-length. I therefore measured the following parameters using the method mentioned above.

6. *Fruit length*, from the base of the apex of the fruit, but not including the trifid style which is sometimes found persisting.
7. *Fruit size* (fruit length × breadth). The length of the fruit as measured above multiplied by its greatest width when the fruit is lying on its broadest face.

Perhaps one of the most interesting features of the fruit is the strong correlation between size and shape as seen in cross-section. (See Fig. 3, a-e). It is at once noticeable that the longer fruits of heterophyllous plants almost always have all three sides of the fruit concave, and that one of them is broader than the other two. The more homophyllous plants tend, on the other hand, to have smaller fruit of a different shape. In this case it exhibits in cross-section two convex sides with the third side concave. This third side is narrower than the other two. The narrowness of the concave side, recognisable in the

fruit of certain plants, was the reason for Lindman (1904) separating *P. calcatum* as a species from the Linnean *P. aviculare* complex. It is difficult to obtain biometric data on variation of the width of this concave side. As there is variation in the narrow side from ' narrow – very narrow – ridge like ' in populations referable to *P. arenastrum* it is considered that *P. calcatum* Lindm. as a taxonomic entity does not exist.

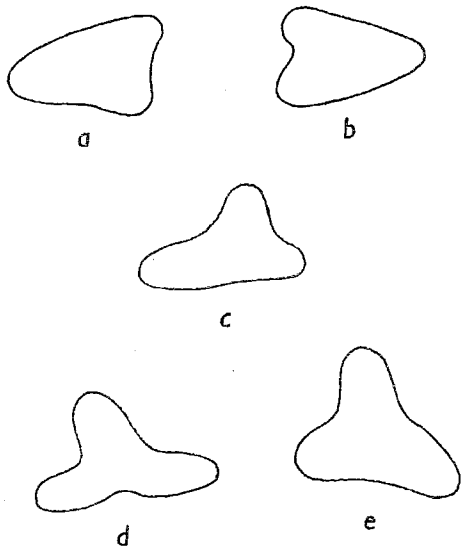


Fig. 3. Camera lucida drawings of cross sections of fruits of *Polygonum* spp., × 8.
(a) *P. arenastrum*, Chedworth, Glos. (b) *P. arenastrum*, Newborough Warren, Anglesey. (c) *P. rurivagum*, Babraham, Cambs. (d) *P. boreale*, Shetland Is. (e) *P. aviculare*, Caernarvon, N. Wales.

The fruits of *P. aviculare, sensu stricto*, are always lustreless and dull with rows of punctate dots. The sides of the fruit are concave. Occasionally four-sided fruits are found. Populations of *P. arenastrum* have fruits which vary considerably from completely shining to shining only on the edges. *P. rurivagum* has fruits which are as long as those of *P. aviculare, sensu stricto*, but narrower; they also are shiny on their edges.

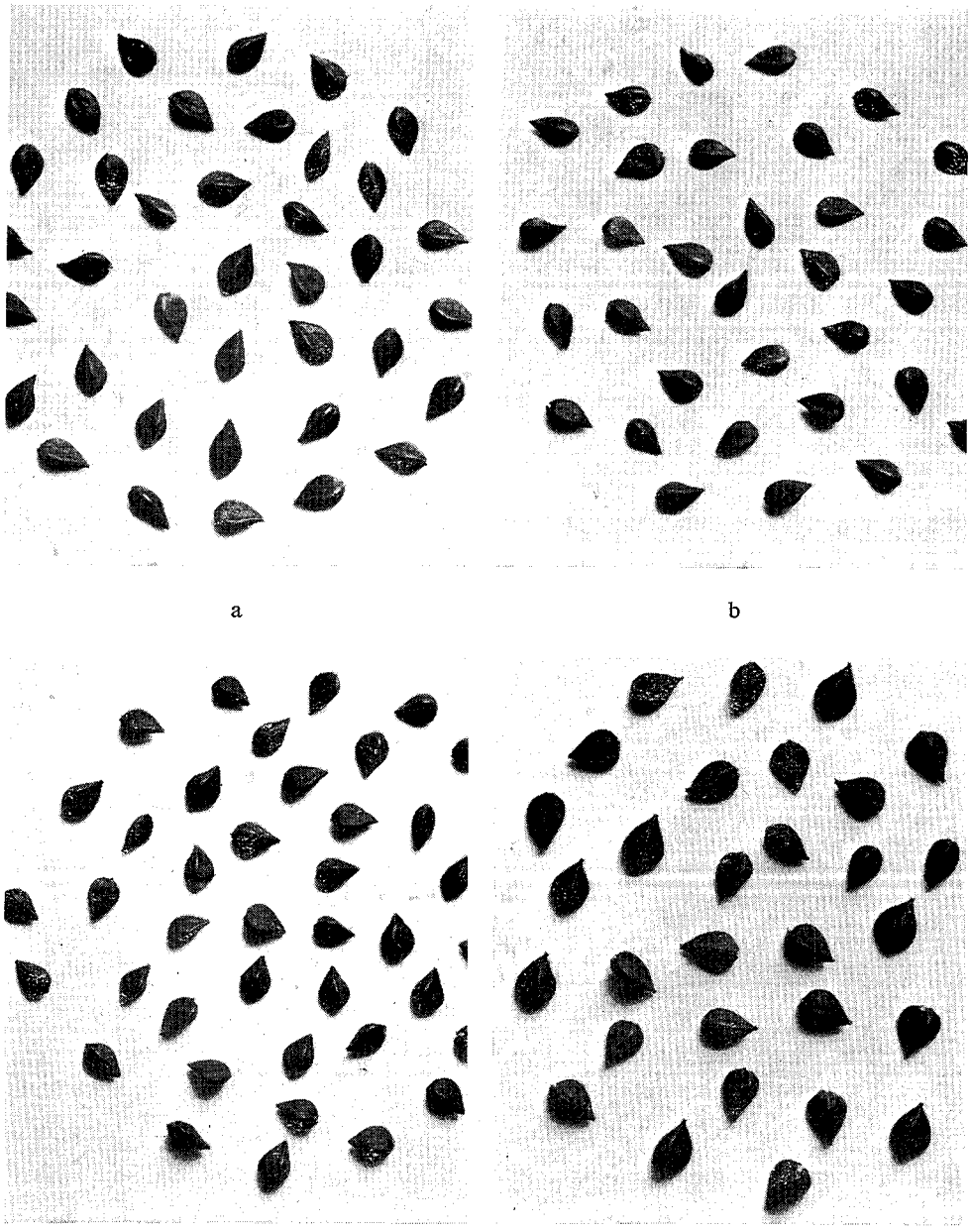
The surfaces of fruits of the two maritime species, *P. raii* and *P. maritimum*, are very distinctly shining and highly polished. This, together with their larger size, makes them distinguishable from plants of *P. aviculare, sensu lato.*

A feature which has caused some difficulty in the past is the fact that the fruits of plants in *P. aviculare sensu lato* may be totally included within the persistent perianth or may project very slightly from it. This has, however, during the course of the work, been found to be variable in any population of either *P. arenastrum* or *P. aviculare, sensu stricto.* The fruits of *P. rurivagum* are always exserted, a point noted by Moss (1914). Those of any single plant are usually all of one type, but even on a single plant there may be variation, since fruits formed late in the year are nearly always slightly exserted. This will be further considered. The fruits of *P. raii* are always markedly exserted from the persistent perianth whereas those of *P. maritimum* are enclosed, or only slightly exserted.

3. Biometrical studies

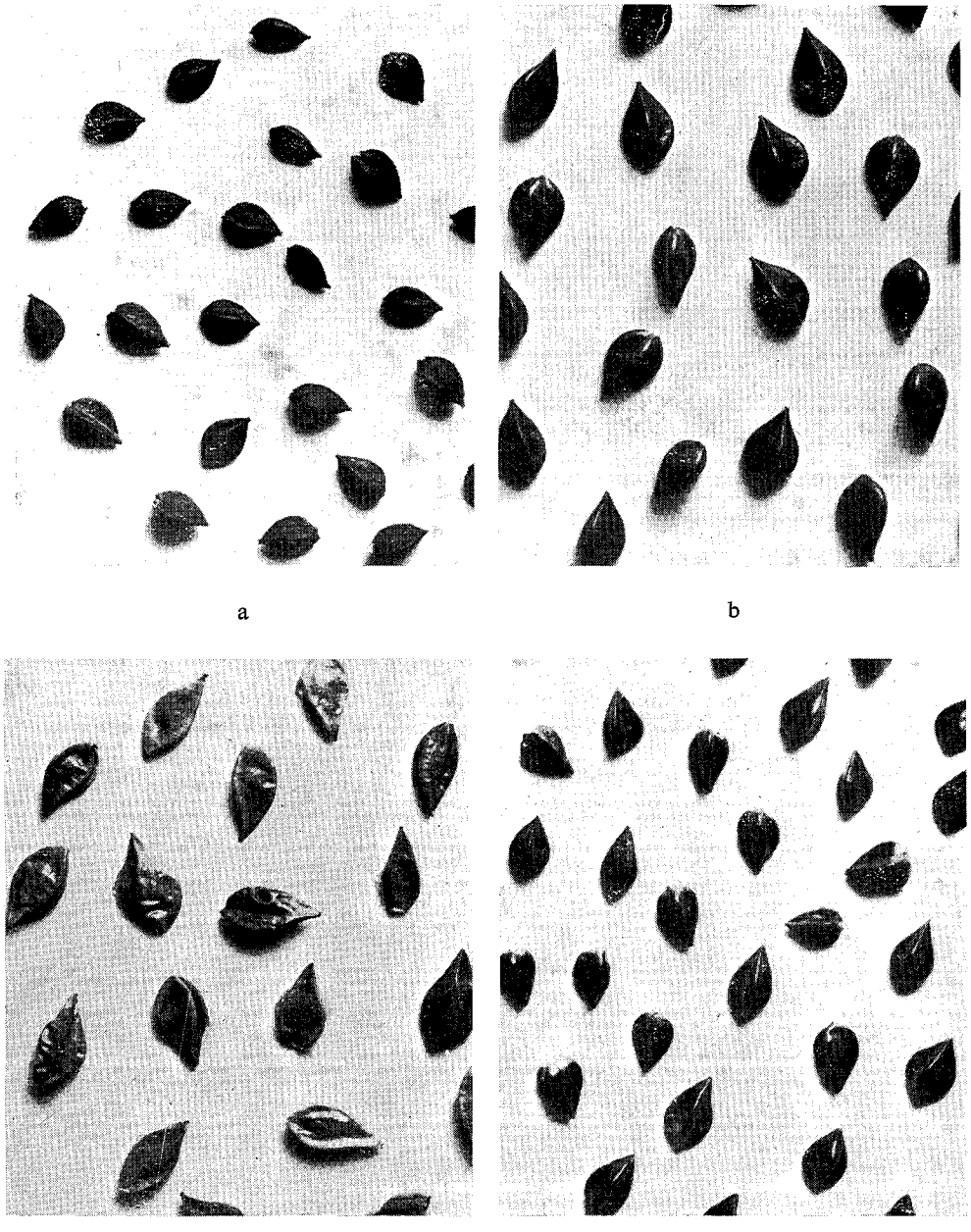
As a basis for my biometrical studies, I decided to take as my primary groups for preliminary investigation those given by Tutin (1952), who has followed in the main the treatment by Moss (1914), in order to see if they presented differences enough to warrant their delimitation as taxa in this country. The groups are *P. heterophyllum* Lindm. (now

PLATE 8



Fruits of *Polygonum* spp., × 2·5. (a) *P. rurivagum*, Babraham, Cambs. (b) *P. arenastrum*, Chedworth, Glos. (c) *P. arenastrum*, Newborough Warren, Anglesey. (d) *P. aviculare*, Brill, Bucks.

PLATE 9



a b

c d

Fruits of *Polygonum* spp., × 2·5. (a) *P. boreale*, Easterhoull, Shetland Is. (b) *P. raii*, Hayling I., S. Hants. (c) *P. oxyspermum*, Laeso, Denmark. (d) *P. maritimum*, Figueira da Foz, Portugal.

P. aviculare, sensu stricto), *P. aequale* Lindm. (now *P. arenastrum*), *P. rurivagum* Jord., *P. calcatum* Lindm. and *P. littorale* Pers. *P. microspermum* was also included as this binomial is given by Dandy (1958). I examined in detail a very large number of specimens of the group from British and European herbaria, to ascertain the variation of the plant from many localities over its entire range in this country and western Europe.

From this study it was apparent that there is a very great variation in general morphology and habit of the plant according to the type of habitat and degree of sheltering, trampling and crowding to which the plants are exposed, and many characters used by previous authors appeared to be very unreliable, or showed such variability from one plant to another as to be taxonomically useless. Certain features of the fruit and persistent perianth which lend themselves easily to biometric treatment were found to be more constant over a larger number of specimens. Measurement made on non-random samples produced evidence that at least three groups could be defined on these characters. The variation patterns, for instance of linear measurements of fruit, perianth-segment- and perianth-length, fruit size and certain ratios, showed marked discontinuities between the three groups. These corresponded to Tutin's *P. heterophyllum*, *P. aequale* and *P. rurivagum*.

A cursory examination also revealed that the larger-fruited *P. heterophyllum* tended to possess leaves of a larger size, whereas *P. aequale* which is small-fruited (by comparison) has shorter, narrower leaves. Thus a possibility existed of correlating the very variable vegetative characters with those of the fruit which are less variable (see scatter diagrams, Figs. 8–10).

I have gathered a large number of random samples from throughout the range of the plant in Great Britain and from as many ecologically different habitats as possible. All species in the group are gregarious and found in patches (often alone on bare ground), or intermixed with other weeds. Sampling was done by gathering plants from a transect cutting through the centre of a patch and from around the edges so that a true representative collection was made of all forms. Composite data for all populations of the four taxa proposed is presented.

In the herbarium the samples were analysed for the quantitative parameters already discussed. Their arithmetical means ($\bar{x}$), standard deviations (σ) and ranges (after Heslop-Harrison 1952) were obtained. Data for a number of samples are presented in Tables 2–6. The same measurements were made on all plants*. Certain other qualitative characters, such as surface-texture and shape of the fruit, which it was not found possible to treat biometrically, have already been discussed.

Analysis of Individual Characters

An idea of the differences between populations of the same group can be gained from a study of Tables 2–6. In these tables the correct names for the groups have been applied and will be used in the discussion here of their variability.

Fruit Characters

Sample data for the linear measurements of the fruits, as seen in the tables, show that the means for the different populations in the same group agree remarkably well in this dimension. i.e. $\bar{x} = 3{\cdot}88$ for the Chedworth population, 3·85 for that of Clevedon and 3·79 for that at Brill (Table 2).

In this research where I have used large samples, the significance of the difference between the means was determined by calculating the standard error of the difference. If the difference between the two means is greater than twice the standard error then the means may be taken to be significantly different ($P = 0{\cdot}05$). The fruit length of *P. arenastrum* is significantly smaller and that of *P. boreale* (Table 5, Shetland plants) significantly larger than *P. aviculare, sensu stricto*. The fruit of *P. rurivagum* is as long as that of *P. aviculare* and the range of variation is almost completely overlapping. The means for the

*The measurements in the tables are given in arbitrary units, where one arbitrary unit = 0·793 mm.

TABLE 2. Statistical data for four random samples of *P. aviculare, sensu stricto*
Measurements in arbitrary units, one unit = 0·793 mm, unless otherwise stated.

Parameter	*Chedworth, Glos.* †$N = 45$			*Clevedon, Somerset** $N = 50$			*Caernarvon** $N = 35$			*Brill, Bucks.* $N = 40$		
	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*
1. Fruit length	3·88	0·61	3·30–4·60	3·85	0·59	3·40–4·45	3·96	0·58	3·40–4·40	3·79	0·71	3·40–4·60
2. Fruit size	9·65	1·48	6·93–12·60	10·41	1·56	9·50–13·60	10·70	1·52	9·36–13·44	9·68	1·48	7·52–12·30
3. Persistent perianth length	5·01	0·57	3·90–5·90	4·96	0·47	4·10–5·80	4·79	0·49	4·00–5·80	4·97	0·44	4·20–5·70
4. Segment length	3·60	0·19	2·50–4·50	3·55	0·16	2·75–4·20	3·37	0·16	2·60–4·25	3·46	0·16	2·70–4·10
5. Per. length/seg. length	1·39	0·21	1·24–1·61	1·41	0·21	1·27–1·60	1·41	0·21	1·27–1·61	1·43	0·20	1·34–1·62
6. Leaf length (cm)	3·28	2·76	2·40–4·50	3·18	2·64	1·82–4·40	3·54	3·20	2·60–5·30	3·09	2·76	1·90–4·20
7. Leaf breadth (cm)	0·82	0·71	0·44–1·35	0·78	0·46	0·58–0·95	0·87	0·77	0·60–1·60	0·75	0·42	0·55–0·98
8. Index of heterophylly	0·63	1·41	1·16–2·32	1·54	1·31	1·21–2·14	1·58	1·32	1·23–2·12	1·51	1·31	1·23–2·05
9. Branch leaf length (cm)	2·00	1·37	1·50–2·80	2·08	1·41	1·50–2·90	2·24	1·48	1·60–3·20	2·03	1·45	1·40–2·80

* As *Polygonum 'littorale'* † N = number of measurements of individual plants for each parameter.

TABLE 3. Statistical data for samples of *P. arenastrum* Bor.
Measurements in arbitrary units, one unit = 0·793 mm, unless otherwise stated.

Parameter	*Oxford (By-pass)* $N = 50$			*Bognor, Sussex* $N = 36$			*Oxford (Jackdaw Lane)* $N = 50$			*Berrow, Somerset** $N = 44$		
	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*
1. Fruit length	3·13	0·56	2·70–3·40	2·73	0·36	2·40–3·10	2·78	0·39	2·30–3·20	3·06	0·47	2·50–3·50
2. Fruit size	6·31	1·34	4·72–7·70	4·58	1·21	3·50–5·51	4·57	1·32	3·10–6·20	5·57	1·35	4·20–7·65
3. Persistent perianth length	3·44	0·59	2·85–3·95	3·14	0·61	2·50–4·00	2·98	0·52	2·30–3·60	3·43	0·54	2·80–4·20
4. Segment length	1·93	0·09	1·45–2·45	1·70	0·08	1·40–2·25	1·75	0·89	1·20–2·20	1·80	0·10	1·30–2·40
5. Per. length/seg. length	1·78	0·15	1·57–2·12	1·85	0·13	1·60–2·10	1·70	0·16	1·50–2·00	1·91	0·18	1·50–2·25
6. Leaf length (cm)	1·68	1·41	1·38–2·40	1·27	1·45	0·97–1·56	1·03	1·84	0·65–1·60	1·36	2·07	0·75–2·10
7. Leaf breadth (cm)	0·43	0·31	0·30–0·58	0·25	0·36	0·12–0·59	0·19	0·30	0·10–0·28	0·37	0·35	0·20–0·60
8. Index of heterophylly	1·31	0·21	1·20–1·61	1·24	0·27	1·00–1·43	1·19	0·21	1·00–1·56	1·15	1·41	0·65–1·85
9. Branch leaf length (cm)	1·10	1·41	0·82–1·50	1·08	1·27	0·78–1·38	0·87	1·31	0·50–1·25	1·18	0·21	1·04–1·68

* As *Polygonum 'littorale'*

TABLE 4. Statistical data for three random samples of *P. rurivagum* Jord.
Measurements in arbitrary units, one unit = 0·793 mm, unless otherwise stated.

Parameter	*Seaford, Sussex* $N = 32$			*Wytham, Berks.* $N = 35$			*Babraham, Cambs.* $N = 50$		
	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*
1. Fruit length	3·86	0·71	3·40–4·80	3·90	0·65	3·40–4·50	3·76	0·48	3·20–4·20
2. Fruit size	8·86	1·39	6·65–11·20	8·52	1·37	6·54–12·10	8·29	1·49	6·08–11·20
3. Persistent perianth length	4·30	0·61	3·60–5·20	3·93	0·52	3·20–4·87	3·77	0·51	3·00–4·50
4. Segment length	2·63	0·10	1·90–3·40	2·48	0·09	1·64–3·20	2·36	0·12	1·70–3·00
5. Per. length/seg. length	1·62	0·19	1·36–1·87	1·63	0·23	1·34–1·88	1·59	0·18	1·37–1·83
6. Leaf length (cm)	2·42	2·59	1·70–3·40	2·84	3·61	1·94–3·96	3·11	3·17	2·60–4·20
7. Leaf breadth (cm)	0·24	0·65	0·15–0·35	0·28	0·74	0·14–0·41	0·31	0·64	0·20–0·45
8. Index of heterophylly	1·68	0·25	1·35–2·43	1·57	0·23	1·24–2·53	1·94	0·28	1·40–2·40
9. Branch leaf length (cm)	2·05	1·58	0·70–1·90	1·77	1·41	1·14–2·09	1·59	1·43	1·28–2·11

TABLE 5. Statistical data for four random samples of *P. boreale* from the Shetland Islands. Measurements in arbitrary units, one unit = 0·793 mm, unless otherwise stated.

Parameter	*Burra Voe* $N = 38$			*Scalloway* $N = 50$			*Easter Quarff* $N = 40$			*Vassa South Nesting* $N = 45$		
	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*
1. Fruit length	4·72	0·83	4·10–5·70	4·14	0·73	3·70–4·60	4·12	0·75	3·80–4·80	4·42	0·81	4·00–5·40
2. Fruit size	12·80	1·54	10·00–18·00	11·49	1·47	8·93–14·95	10·80	1·39	8·80–12·20	11·73	1·50	9·76–16·31
3. Persistent perianth length	5·90	0·54	4·80–7·30	5·35	0·57	4·50–6·30	5·35	0·52	4·60–6·10	5·49	0·52	4·42–7·10
4. Segment length	4·30	0·15	3·30–5·60	3·95	0·12	3·20–4·80	3·88	0·12	3·20–4·60	4·04	0·13	3·20–4·70
5. Per. length/seg. length	1·35	0·11	1·25–1·45	1·35	0·13	1·25–1·44	1·37	0·12	1·30–1·47	1·35	0·12	1·25–14·7
6. Leaf length (cm)	3·45	3·10	2·70–4·40	3·52	3·92	2·70–5·00	3·28	3·51	2·30–4·50	3·29	3·40	2·55–4·15
7. Leaf breadth (cm)	1·15	0·51	0·90–1·50	1·17	0·54	0·80–1·70	1·14	0·55	0·75–1·65	1·14	0·55	0·83–7·04
8. Index of heterophylly	1·48	0·31	1·22–1·90	1·84	0·35	1·47–2·31	1·91	0·42	1·20–2·30	1·52	0·41	1·20–2·27
9. Branch leaf length (cm)	2·32	1·42	1·90–2·70	1·91	1·71	1·50–2·80	1·71	1·45	1·47–2·57	2·02	1·68	1·75–2·64

TABLE 6. Composite statistical data for the four taxa, *P. aviculare*, *P. arenastrum*, *P. rurivagum*, *P. boreale* (all samples)
Measurements in arbitrary units, one unit = 0·793 mm, unless otherwise stated.

Parameter	*P. aviculare, sensu stricto*			*P. arenastrum*			*P. rurivagum*			*P. boreale*		
	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*
1. Fruit length	3·86	0·62	3·40–4·50	2·92	0·37	2·45–3·40	3·83	0·66	3·32–4·50	4·35	0·74	3·95–5·20
2. Fruit size	10·00	1·50	8·00–12·78	5·30	1·34	2·85–6·76	8·55	1·36	6·42–11·70	11·75	1·54	9·51–15·42
3. Persistent perianth length	4·96	0·48	4·03–5·80	3·33	0·53	2·61–3·93	4·00	0·55	3·26–4·84	5·54	0·51	4·65–6·55
4. Segment length	3·47	0·16	2·60–4·26	1·78	0·09	1·34–2·32	2·49	0·10	1·74–3·20	4·05	0·15	3·50–5·26
5. Per. length/seg. length	1·33	0·20	1·28–1·61	1·80	0·15	1·53–2·12	1·61	0·18	1·35–1·86	1·35	0·12	1·25–1·45
6. Leaf length (cm)	3·30	3·63	2·31–4·66	1·33	2·47	0·93–1·92	2·78	3·14	2·08–3·84	3·42	3·32	2·60–4·70
7. Leaf breadth (cm)	0·82	0·64	0·53–1·35	0·28	0·35	0·18–0·52	0·27	0·66	0·16–0·40	1·15	0·54	0·82–1·62
8. Index of heterophylly	1·57	1·30	1·21–2·16	1·21	0·24	1·05–1·61	1·73	0·25	1·33–2·45	1·74	0·35	1·29–2·18
9. Branch leaf length (cm)	2·09	1·42	1·50–2·93	1·06	1·30	0·68–1·49	1·80	1·45	1·04–2·03	1·98	1·48	1·63–2·69

aggregate data can be seen in Table 6. There is a significant difference between the means 3·86 for *P. aviculare, sensu stricto* and 2·92 for *P. arenastrum*. Fruits from plants that I gathered in Brill (Table 2) and grew the next year in the experimental garden showed a range in length from 3·50 to 4·50, and plants from fruits collected on the Oxford by-pass gave offspring with the same range in fruit-length as the parent plants. This character therefore appears to be very stable under different conditions.

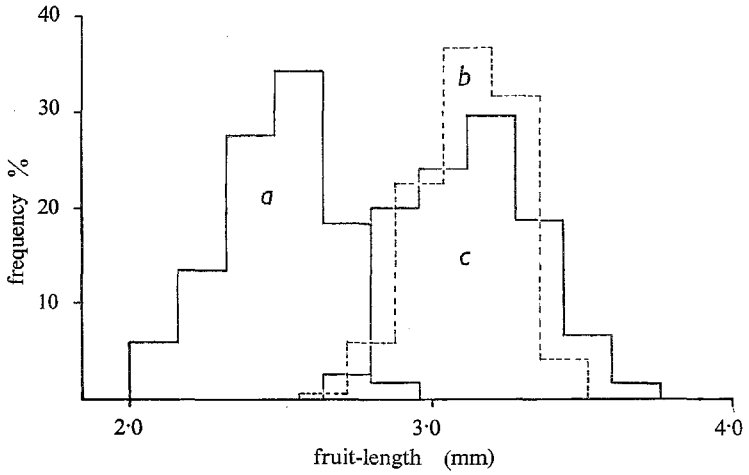


Fig. 4. Variation in fruit-length in (a) *P. arenastrum*, (b) *P. rurivagum* and (c) *P. aviculare*.

Fruit-length and -breadth have been multiplied together to give numbers which express size more adequately than either linear dimensions. The fruits of *P. boreale* are both broader and longer than those of *P. aviculare*; the product is therefore greater. Although there is some degree of overlap the two have significantly different means. Variation in fruit size between *P. arenastrum* and *P. aviculare* is almost discontinuous.

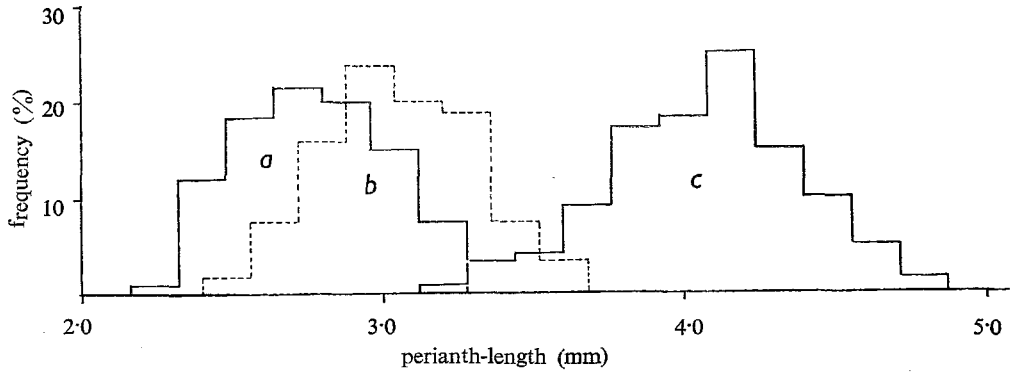


Fig. 5. Variation in perianth-length of (a) *P. arenastrum*, (b) *P. rurivagum* and (c) *P. aviculare*.

Perianth Characters

The variation of perianth-length in the different groups follows the same pattern as fruit length. From the tables it is seen that perianths of *P. aviculare, sensu stricto* are longer ($\bar{x} = 4{\cdot}96$) than those of *P. arenastrum* ($\bar{x} = 3{\cdot}33$) and *P. rurivagum* ($\bar{x} = 4{\cdot}00$). The

distributions of the last two are almost coincident (Fig. 5). Perianth-length in *P. boreale* ($\bar{x} = 5{\cdot}40$) is the longest in the group and differs significantly from that of *P. aviculare* although there is again some overlap in the variation Fig 6. The range of this character in the group is great.

The length of the tube in relation to the total length of the perianth is very interesting and significant in the taxonomy of the group. This relationship has been expressed as a ratio. In *P. arenastrum*, which has a comparatively short perianth and long fused portion, up to half its length, with consequently shorter perianth segments, this ratio approaches and exceeds, in some cases, 2 in the fruiting stage. *P. aviculare*, on the other hand, has a longer perianth and short tube with correspondingly longer perianth segments. In this species the ratio is nearer unity. Study of the results shows that *P. aviculare, sensu stricto* has a mean value of 1·33, whereas in *P. arenastrum* it is as high as 1·80. Variation in this ratio is great, however (see Fig. 7, and Tables 2–4). The population of *P. arenastrum* from Berrow showed variation from 1·50 to 2·25, and another from Oxford (By-pass) varied from 1·57 to 2·12. In *P. aviculare* the Chedworth population varied from 1·24 to 1·61, and that from Brill between 1·34 and 1·62. From the histogram of the variation of this ratio it is clear that two well defined groups may be demarcated. *P. rurivagum* has, as already stated, a perianth length approaching that of *P. arenastrum* ($\bar{x} = 4{\cdot}00$ and 3·33 for aggregate data) but has the short tube of *P. aviculare*. In respect of this ratio, therefore, *P. rurivagum* is intermediate and the mean value from the composite data is 1·61.

The length of the perianth segments is greatest in flowers of *P. boreale* ($\bar{x} = 4{\cdot}05$);

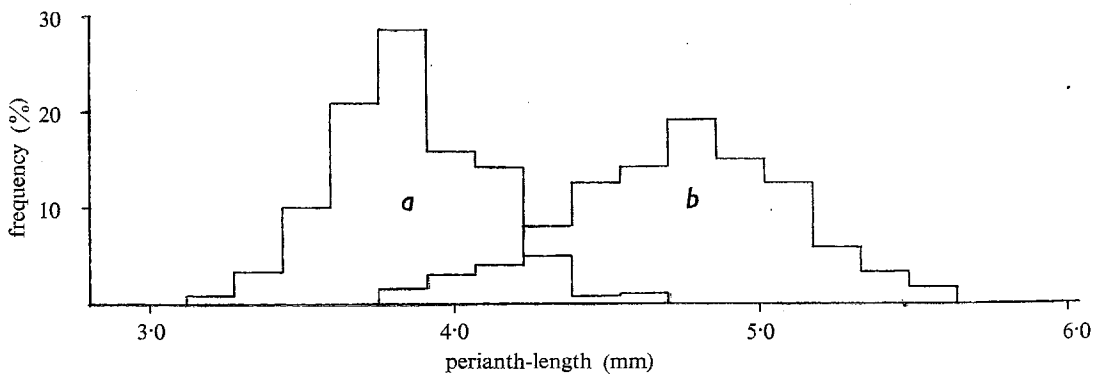


Fig. 6. Variation in perianth-length of (a) *P. aviculare* and (b) *P. boreale*.

this is significantly different from the mean (3·47) for *P. aviculare, sensu stricto* (see Tables 2, 6). The shortest perianth segments occur in *P. arenastrum* with $\bar{x} = 1{\cdot}78$.

Lindman (1904) mentions that *P. calcatum* has the perianth fused up to half its length whereas *P. aequale* has the perianth segments as long as the fused portion or twice as long (see Table 3). Therefore the ratio mentioned above should always be approximately 2 for *P. calcatum* whereas that for *P. aequale* would be more variable. In no population have I found this to be constantly the case and as already mentioned this ratio varies considerably, from 1·50 to 2·20, and there is variation from one flower to another on the same plant.

Vegetative Characters

The four species may be identified on leaf size and shape, although as previously pointed out these characters must be used with caution. Populations of *P. aviculare sensu lato* are extremely variable (Styles 1960); from the tables it is seen that plants of *P. rurivagum*

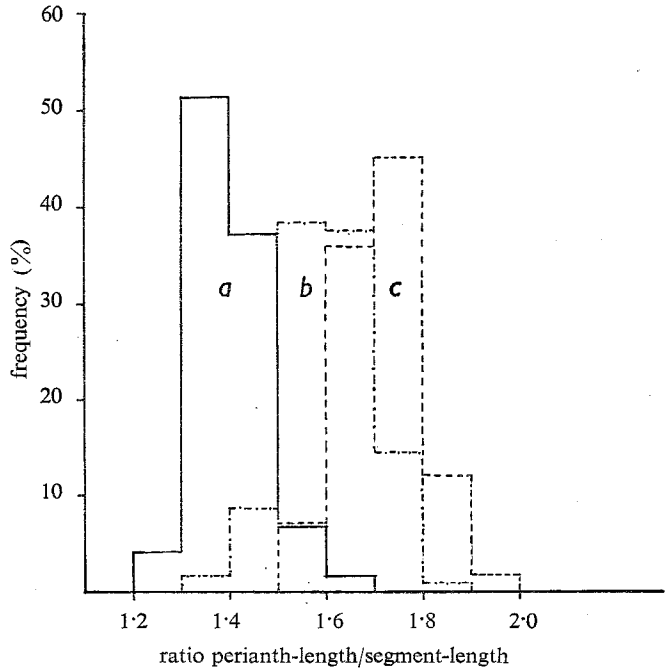


Fig. 7. Variation in the ratio perianth-length: segment-length in (a) *P. aviculare*, (b) *P. rurivagum* and (c) *P. arenastrum*.

are separable from those of *P. aviculare* on leaf breadth, ($\bar{x} = 0{\cdot}27, 0{\cdot}82$), although on this character alone they would be indistinguishable from *P. arenastrum* ($\bar{x} = 0{\cdot}28$). The leaves of *P. rurivagum* are, however, longer, $\bar{x} = 2{\cdot}78$ to $\bar{x} = 1{\cdot}35$ in *P. arenastrum*, and there would be no difficulty in recognizing either in the field. From the Index of Heterophylly for the four species it is seen in the tables that *P. arenastrum* is more homophyllous than the others, although this feature varies widely from population to population owing to factors already mentioned (p. 183).

TABLE 7.

Parameters of population of plants from Arthur's Seat, Edinburgh named *P. calcatum* ($N = 25$)

Measurements in arbitrary units, unless otherwise stated.

Parameter	$\bar{x}$	σ	*range*
Fruit length	2·98	0·58	2·40–3·40
Fruit size (l. × b.)	6·22	1·34	4·65–7·80
Persistent-perianth length	3·57	0·63	2·90–4·20
Segment length	1·96	0·12	1·70–2·60
Per. length/Seg. length	1·71	0·13	1·55–2·05
Stem leaf length (cm)	1·63	2·10	1·25–2·58
Leaf breadth (cm)	0·33	0·32	0·22–0·47
Index of heterophylly	1·36	0·21	1·20–1·44
Branch-leaf length (cm)	1·24	1·38	1·05–1·48

In Table 7 are presented data for a population from Arthur's Seat, Edinburgh (v.c. 83). Mr. B. L. Burtt tells me that they were gathered from a spot which is 'traditionally' known as a station for *P. calcatum*. The appearance of the plants in the first instance gave me no reason to suspect that they were any different from plants in other populations named *P. arenastrum*. This proved to be the case when I examined certain of the characters quantitatively. None of the significant characters mentioned by Lindman could be seen only in these plants and not in others. The same is true of samples of Lindman's own specimens obtained from Stockholm.

Some British authors have taken *P. calcatum* to have fruits which are two-sided (bi-convex) instead of normally 3-sided. During my biometrical analysis of many populations of *P. arenastrum* I discovered that a certain percentage of fruits of this species were always bi-convex, the highest being for a sample of plants collected from the sand-dunes at Berrow, Somerset with 7·72% (see Table 8). These are not constantly found on single plants, and when I raised plants from 10 of such fruits they yielded normal trigonous fruit. This atypical fruit shape is almost certainly due to their development from ovaries with two styles instead of three.

TABLE 8.

Percentage of bi-convex fruits in populations of *P. arenastrum*

Sample	*No.*	*% of population*
Jackdaw Lane, Oxford v.c. 23	5	2·70
Berrow v.c. 6	17	7·72
Bognor Regis v.c. 14	12	6·60
Oxford by-pass v.c. 23	8	2·20

In 1958 I obtained from the Jardin Botanique de l'État, Brussels (**BR**), six authentic specimens of Jordan's *P. microspermum*. I have analysed these biometrically in order to ascertain whether they are in fact different morphologically from small plants in populations I had named *P. arenastrum* (see Table 9).

TABLE 9.

Statistical data from six herbarium specimens named by Jordan
P. microspermum

Measurements in arbitrary units, unless otherwise stated.

Parameter	$\bar{x}$	σ	*range*
Fruit length	2·94	0·35	2·70–3·40
Fruit size (l. × b.)	5·94	1·38	4·48–6·40
Persistent-perianth length	3·12	0·51	1·80–3·70
Segment length	1·70	0·12	1·60–1·90
Per. length/Seg. length	1·68	0·18	1·50–1·85
Stem-leaf length (cm)	1·02	1·81	0·94–1·35
Leaf breadth (cm)	0·15	0·25	0·10–1·28
Index of heterophylly	1·10	0·25	1·00–1·25
Branch-leaf length (cm)	0·92	1·27	0·72–1·24

Even though this sample is very small, from the data for fruit and perianth characters there is no evidence that these plants form a distinct taxon, or that the plants are any different from ones which fall in the normal range of *P. arenastrum.*

As already indicated the fruits of the four species in the *P. aviculare* aggregate differ somewhat in shape and this is, in some respects, a more useful discrimination than size. Unfortunately, however, no method of presenting this feature in quantitative terms could be devised.

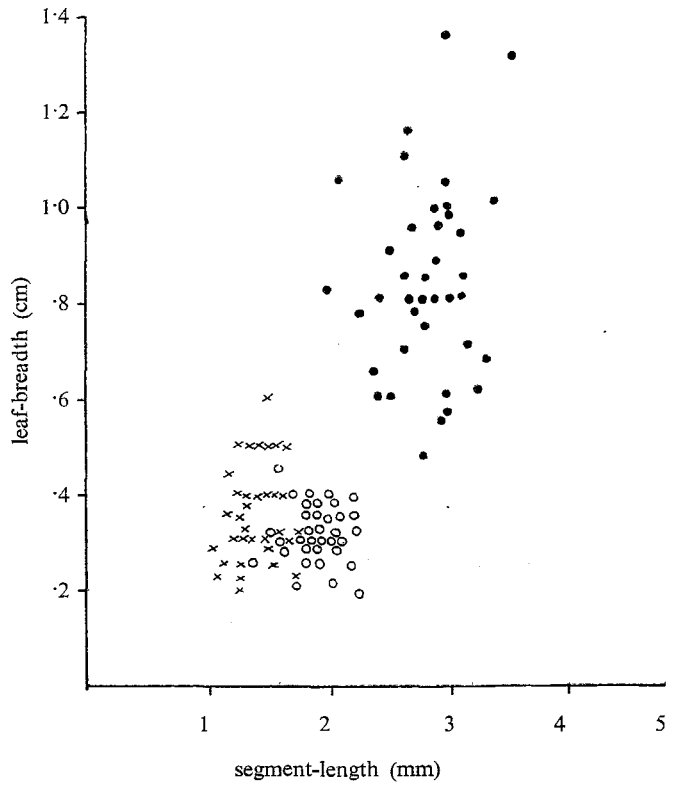


Fig. 8. Scatter diagram to show the relationship between leaf-breadth and segment-length in *P. aviculare* (solid dots), *P. arenastrum* (crosses) and *P. rurivagum* (open circles).

From Fig. 8 separation of the three species *P. aviculare*, *P. arenastrum* and *P. rurivagum* is possible using leaf breadth and perianth-segment length. Fig. 9 deals with the separation of *P. arenastrum* and *P. aviculare, sensu stricto* on leaf-length and the size of the fruit. *P. boreale* may be distinguished from *P. aviculare* in general by the larger size of its floral and fruiting parts, although the separation is not complete on these characters alone (Fig. 10).

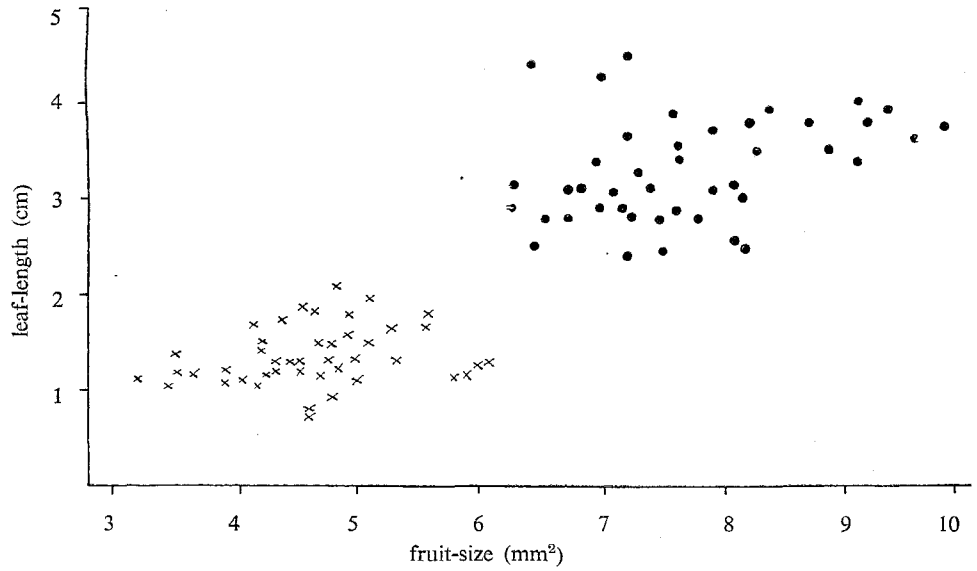


Fig. 9. Scatter diagram to show the relationship between fruit size and leaf length in *P. aviculare* (dots) and *P. arenastrum* (crosses).

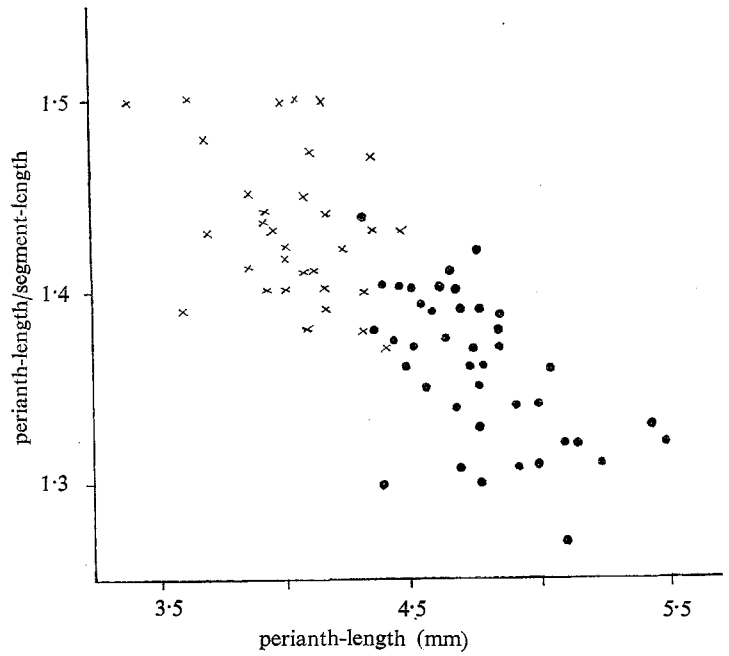


Fig. 10. Scatter diagram to show the relationship between perianth-length and the ratio perianth-length : segment-length in *P. aviculare* (crosses) and *P. boreale* (dots).

TABLE 10. Chromosome records in the section *Polygonum* (all diploid members, 2*n*).

Species	*Jaretzky (1928) (Germany)*	*A. and D. Löve (1942b) (Scandinavia)*	*Andersson (1942, 1948) (Scandinavia)*	*Pólya (1948) (Hungary)*	*A. and D. Löve (1956a and b) (Canada & Iceland)*	*Pauvels (1959) (Belgium)*	*Scholz (1960) (Germany)*	*Styles (Great Britain)*
P. aviculare, sensu lato	40	40	40, 60	40	20, 40, 60	40, 60	40, 60	40, 60
P. aviculare, sensu stricto (*P. heterophyllum*)		40	60		60	60	60	60
P. arenastrum (*P. aequale*)			40		40	40	40	40
P. rurivagum					20		60	60
P. boreale					60 (Iceland and Canada)			40
P. littorale					60			
P. calcatum					40		40	
P. raii					60	40		40 (also Norway)
P. maritimum	20 (Rome)							20 (also Portugal and France)
P. oxyspermum					80			40 Denmark
P. neglectum					40			

4. Cytology and breeding systems

Chromosome Numbers

Results of previous cytological investigations on *Polygonum aviculare* and its allies are summarized in Table 10. Jaretzky (1928) confined his work to six species which he apparently obtained from botanic gardens rather than natural habitats. As he gives no details of the morphology of the plants he studied the value of his observations is very limited. The tetraploid number for his species *P. monspeliense* Pers. is surprising, since the type of this plant is easily referred to *P. aviculare, sensu stricto*, and might have been expected to be hexaploid. The tetraploid number is given for a form of *P. aviculare*, to which, he states, he is unable to give a name as he is not conversant with the very many varieties of this species.

A. & D. Löve (1942a) working in Sweden record the tetraploid number for plants labelled '*P. aviculare*' with a remark that the specimens studied seemed to be nearer *P. heterophyllum* Lindm. In a later publication (1956), however, they state that the identification of the voucher specimens was erroneous since they belong to *P. neglectum* Bess. As this species has never been mentioned in any Scandinavian Flora its existence here is considered most doubtful. Andersson (in A. & D. Löve 1942b) published the numbers $2n = 40$, 60 for plants in *Polygonum aviculare, sensu lato* and later in A. & D. Löve (1948) gave the former number for plants identified as *P. aequale* and the latter for plants approaching *P. heterophyllum.*

Both Pólya (1948) and Pauvels (1959) have published results consistent with these findings, and the latter also discovered *P. raii* new to Belgium with a chromosome number of $2n = 40$.

The most important work published on the cytogenetic and taxonomic variability within and between species of *Polygonum* is that by A. & D. Löve (1956a) on the Icelandic flora and (1956b) on plants in eastern North America. As will be seen from the table several of their chromosome counts do not agree with my own or those of other workers in this field. Perhaps the most interesting is the fact that they record the diploid number of $2n = 20$ for *P. rurivagum* with the other species in the aggregate forming a polyploid series with an octoploid of $2n = 80$. The littoral species *P. raii* is also given as hexaploid with $2n = 60$, as is *P. boreale* from Iceland. In both these reports the nomenclature is confused and will be discussed later.

Very recently Scholz (1960) has published chromosome counts substantiating my own records.

Cytological investigations on the British taxa recognised in *P. aviculare, sensu lato* were carried out on germinating seedlings, fruits having been gathered from naturally occurring populations, widely distributed ecologically and geographically. Plants of the littoral species *P. raii*, *P. maritimum* and *P. oxyspermum* have been examined from only a limited number of populations. This was due mainly to the fact that, in the case of the first two, the species are rare or very rare, and in the last because authentic material from stations abroad was not forthcoming, although the greatest possible effort was made to obtain viable seed from several north-European and Scandinavian countries. Great difficulties were experienced in obtaining a sufficient germination, and a method following that published by Justice (1941) was finally used to raise the germination rate to about 60%.

A method of obtaining metaphase chromosome counts was developed from squash techniques following Darlington & La Cour (1947). Translucent root-tips were treated in 1% colchicine or *p*-dichlorobenzene for 12 to 24 hours and chromosomes stained using the Feulgen technique, with 6–8 minutes hydrolysis. The chromosomes are extremely small with a slight variation in size from 0·8–1·2 μ. Lists of the British taxa with their chromosome numbers are given in Tables 11 and 12.

The diploid number $2n = 20$, given by A. & D. Löve for *P. rurivagum*, was not found in any British populations of this species which all proved to be hexaploid with $2n = 60$. This agrees with the results of Scholz (1960). As the British plants agree very well morpho-

TABLE 11.

Chromosome records of species recognized in *P. aviculare, sensu lato* in Britain.

Species	*Locality*	*v.c.*	*Chromosome number 2n*
P. aviculare, sensu stricto	Foreshore shingle, Caernarvon	49	60
	Farmyard, University Farm, Wytham	22	60
	Waste ground, building site, Brill	24	60
	Entrance to gateway, Chedworth, Glos.	33	60
P. arenastrum	Between flagstones, northern by-pass, Oxford	23	40
	Sand dune, path to sea, Berrow, Somerset	6	40
	Rough cart track, Bodmin, Cornwall	2	40
P. rurivagum	Barley stubble, Gog Magog Hill, Cambs.	29	60
	Chalky cornfield, Seaford, Sussex	14	60
	Bean field, University Farm, Wytham	22	60
P. boreale	Shetland Islands	112	40

TABLE 12

Chromosome records for British and European plants of *P. maritimum*, *P. raii* and *P. oxyspermum*

Species	*Locality*	*Origin*	*Chromosome number 2n*
P. maritimum	Sea shore, Herm	Channel Isles	20
	Sea shore, Figueira da Fóz	Portugal	20
	Banyuls, Pyrenees	S. France	20
P. raii	Shingle, West Town, Hayling Island, Hants. (v.c. 11)	England	40
	Sandy beach, Maenporth, Cornwall (v.c. 2)	England	40
	Sands, Tromsoe Island	Norway	40
P. oxyspermum	Leudrig Strait, Laeso, Copenhagen	Denmark	40

logically with specimens of the same name from Jordan's herbarium at Lyon it can only be supposed that the Canadian plant is something other than *P. rurivagum* Jord. and perhaps indigenous there. Plants of *P. arenastrum* and *P. aviculare* from this country were consistently found to be tetraploid and hexaploid respectively. Specimens from populations of varying morphology of the two species were studied and counts were made on as many root tips as possible per population. Plants of *P. boreale* obtained from the Shetland Isles through the courtesy of Mr. W. Scott were consistently found to be tetraploid with $2n = 40$. This observation does not agree with that of A. & D. Löve. The identification of their plants is however suspect. Among weedy species of *Polygonum*, therefore, there do not appear to be any intraspecific chromosome races.

Diploid ($2n = 20$) and tetraploid ($2n = 40$) numbers were found in *P. maritimum* and *P. raii* respectively in both British and European populations whilst a single population of *P. oxyspermum* from Denmark was also tetraploid.

The number for *P. maritimum* thus agrees with the observations of Jaretzky on plants from the Mediterranean. The number for *P. raii* and *P. oxyspermum* differ from the $2n = 60$ and 80 respectively given by A. & D. Löve. These authors mention that eastern Canadian plants of *P. raii* come nearer the race named subsp. *norvegicum* Sam. which is stated to be more northern, having blue-green foliage, shorter internodes, flowers which are white rather than pink or greenish white, and somewhat broader achenes. They suggest that there may be two races of differing chromosome numbers: a British–west-European–Channel race which is tetraploid and a northern Scandinavian and east Canadian race which is hexaploid. My own counts on Norwegian plants do not, however, support this view. It is possible that the Canadian populations do differ from the European ones in chromosome number; the same may be true of *P. oxyspermum*, but my efforts to obtain viable fruits of these species from several Canadian botanical institutions were unsuccessful.

Both Andersson and A. & D. Löve record $2n = 50$ for supposed hybrids between *P. aviculare*, *sensu stricto* and *P. arenastrum* but I have never met with a plant I suspected to be a hybrid either from its morphology or its chromosomes.

Breeding Systems

P. aviculare agg. and the other species of this section are inbreeding and the flowers appear to be always self-fertilized. This mechanism leads to difficulties in their taxonomy. On many occasions populations have been carefully observed in the field, but no insect visitors have been recorded. The flowers are scentless and their inconspicuous size, colour, and position on the plant show no adaptations to out-breeding. Frequently in the course of emasculation experiments unopened buds were found to contain two or three stamens already dehisced, and many flowers especially at the ends of the older branches open when still enclosed in the ochreae. They then behave as though they were cleistogamous.

My own attempts to obtain hybrids between the various species in the aggregate were not conclusive, due mainly to technical difficulties. Such results as were obtained suggested that hybridity is extremely rare among species of this group.

A. and D. Löve (1956b) have pointed out that a low degree of apomixis cannot be ruled out. I could not verify this suggestion but I am of the opinion that it does not occur in this group. It is in any case extremely rare among annual weeds (Warburg 1960). The condition whereby the fruits formed in late autumn become swollen and much exserted from the persistent perianth does not so far as I am able to tell have anything to do with apomixis. The embryos and endosperm of these fruits appear to be almost twice as large as normal and they are not as A. & D. Löve state 'inflated and mostly empty.' Samples of these swollen fruits from several populations were grown in the experimental garden at Oxford but the plants raised from them were normal in every way. I can offer no explanation for this abnormal development, and I know of no cases of similar developments among other genera.

The possible origin of these species in the *P. aviculare* aggregate presents an interesting problem. Many plants are known to have spread from their original areas through the induction of polyploidy (*Poa* spp., *Paeonia* spp.). It is interesting to note that the mediterranean species *P. maritimum* never behaves as a weed and only survives in a natural (littoral) habitat. It is thought that weedy species have been derived through hybridization and allopolyploidy of this diploid with one or more unknown species. The place of origin of the weedy species of *Polygonum* is, however, uncertain. It is interesting to note that certain North American diploid species (e.g. *P. achoreum* Blake, *P. buxiforme* Small and *P. prolificum* (Small) Robins) are also confined to maritime zones such as sand-dunes and salt-marshes.

5. Taxonomic revision and discussion

From the morphological and cytological evidence presented it is clear that the differences between the groups which can be delimited as species within *P. aviculare, sensu lato* are relatively clear-cut and well defined. This is perhaps surprising, considering the chaos and uncertainty which exist in many floras regarding the number of taxa which can be recognized in this group. It is now proposed to discuss very briefly the chief causes of difficulty in the taxonomy of *P. aviculare*, and the reasons for calling the groups species. Finally an account of the taxonomy of the group as it now stands after this revision is presented. The synonomy is complete except for some varietal names, which, however, have not been used in accounts of *Polygonum* in the British flora.

I have found the fruit and persistent perianth the most useful and stable criteria in the group and they are the most reliable for classification. There is, however, wide variation in size even on a single plant, and the extent of this can only be ascertained by extensive measurements. The fruits are inconspicuous and concealed in the more evident vegetative parts of the plant. Old plants of *P. aviculare, sensu lato* are especially difficult to identify since they are frequently reduced to bare stems by the dropping off of the leaves. All species therefore tend to have the same facies and the fruits are then the only guide.

Care must also be exercised with specimens gathered in the late autumn because of the enlargement of the fruit, a condition mentioned previously. Maritime forms of *P. aviculare* in this condition have frequently been called *P. raii*.

A. & D. Löve mention that the recognition of the tetraploid *P. arenastrum* and hexaploid *P. aviculare* as species is 'beyond discussion.' I am in full agreement with these authors on this point. Not only are they morphologically distinct on a number of reliable taxonomic characters but the numerical chromosome differences result in an effective sterility barrier. Hybrids between them appear to be extremely rare in nature. The two species have also different ecological niches, though some intermingling does occur.

P. rurivagum has the same chromosome number as *P. aviculare* but my hybridization experiments have shown that there is probably a sterility barrier. Morphologically the plant differs from the other taxa in a number of characters. The extreme narrowness of the leaves, the longer ochreae and short perianth serve to distinguish it from typical forms of *P. aviculare, sensu stricto*. Both occur in cultivated fields but remain distinct. *P. rurivagum* seems, also, to be confined to basic soils in this country and west Europe and has a limited distribution.

Plants of *P. boreale* are among the most robust I have found in the aggregate. This is surprising since it is the most northerly of all the species. *P. boreale* is separable from all the others by the large size of the fruit and perianth, and is recognized as a species mainly because it differs in having the very evidently petiolate leaves and the tetraploid chromosome number.

P. arenastrum is perhaps the most distinct morphologically of all the species in the aggregate. *P. aviculare* and *P. rurivagum* are probably closely related. *P. boreale*, though tetraploid, exhibits many of the features of *P. aviculare*. *P. maritimum* and *P. raii* are less variable than the weedy species in the group; this is possibly due to the fact that they are

always confined to littoral habitats. The differences between them are well-marked. Hybrids of these have not, so far as I can trace, ever been recorded.

1. P. AVICULARE L., Spec. Pl., 362–3 (1753).

P. centinodium Lam., Fl. Francaise **3**: 237–8 (1778). nom. illegit.

P. erectum Roth., Beitr. Bot. **2**: 131 (1783) nom. illegit.

P. monspeliense Pers., Synop. Plant. 439 (1805).

P. aviculare var. *vulgare* Desv., Obs. Pl. Angers 98 (1818).

P. aviculare var. *littorale* Koch, Syn. Fl. Germ. Helv. 618 (1837).

P. aviculare var. *polycnemiforme* Lecoq & Lamotte, Catal. Rais. Pl. 322 (1848).

P. provinciale K. Koch, Linnaea **22**: 204 (1849).

P. aviculare β *erectum* Ledeb., Fl. Ross. **3**: 532 (1850).

P. aviculare δ *vegetum* Ledeb., Fl. Ross. **3**: 532 (1850).

P. aviculare var. *angustissimum* Meisn. in DC. Prodr. **14**: 98 (1856).

P. denudatum (Desv.) Bor., Fl. Centre France, Ed. 3, **2**: 559 (1857).

P. agrestinum Jord. ex Bor., Fl. Centre France, Ed. 3, **2**: 559 (1857).

P. polycnemiforme (Lecoq & Lamotte) Bor., Fl. Centre France, Ed. 3, **2**: 559 (1857).

P. humifusum Jord. ex Bor., Fl. Centre France, Ed. 3, **2**: 559 (1857) nom. illegit.

P. heterophyllum Lindm., Svensk Bot. Tidskr. **6**: 690–1 (1912) nom. illegit.

P. aviculare subsp. *heterophyllum* (Lindm.) Aschers. & Graebn., Synops. Mitteleur Fl. **4**: 848 (1913).

P. aviculare subsp. *rectum* Chrtek, Preslia **28**: 365 (1956).

P. aviculare subsp. *monspeliense* (Pers.) Chrtek, Preslia **28**: 365 (1956).

P. rectum (Chrtek) Scholz, Ber. Deutsch. Bot. Ges. **72**: 65–66 (1959).

[*P. littorale* auct.].

Annual. Plant robust, erect, prostrate or spreading, heterophyllous when young; stems up to 2 m long. Leaves lanceolate to ovate-lanceolate, 2·5–5 cm × 1·5 cm, subacute, those of the main stems 2–3 times as long as those of the flowering branches: petioles short (up to 2 mm) or almost absent, included in the ochreae. Ochreae silvery when young, *c.* 6 mm, becoming lacerate with age. Inflorescence 3–6-flowered. Perianth-segments united at the base only, distinctly veined and overlapping in fruit, pink, purple or white at the edges. Stamens (5)–8–(9). Fruit 2·5–3·5 mm, half as broad, punctate, dull brown, with three ± equal concave sides, (rarely 4-sided), included or sometimes slightly projecting from the persistent perianth. Flowering the whole season, from July to November.

Holotype in the Linnean Herbarium (**LINN**), London.

2. P. ARENASTRUM Bor., Fl. Centre France, Ed. 3, **2**: 559 (1857).

P. microspermum Jord. ex Bor., Fl. Centre France, Ed. 3, **2**: 560 (1857).

P. calcatum Lindm., Bot. Not. 139 (1904).

P. aequale Lindm., Svensk Bot. Tidskr. **6**: 692 (1912).

P. aviculare subsp. *aequale* (Lindm.) Aschers. & Graebn., Synops. Mitteleur. Fl. **4**: 848 (1913).

P. aviculare subsp. *calcatum* (Lindm.) Thell., Ber. Schweiz. Bot. Ges. **22**: 120 (1913).

P. × *lindmanii* Druce Rep. Bot. Soc. Exch. Cl. **8**: 873 (1928).

[*P. aviculare* subsp. *aviculare sensu* Chrtek, Preslia **28**: 366. (1956)].

[*P. aviculare* auct. (Komarov 1936, Lembke 1948, A. & D. Löve 1956a & b) non L.].

Annual. Plant usually 5–50 cm, forming a dense prostrate mat or sometimes erect. Leaves elliptic or elliptic-lanceolate, up to 2 cm long and 0·5 cm wide, those of the main stem and flowering branches ± equal in size, subsessile. In old specimens the leaves are often more or less crowded towards the ends of the branches. Ochreae short, *c.* 4 mm. Inflorescence 2–3-flowered. Flowers smaller than in *P. aviculare*; stamens (4)–5–(8). Segments of the persistent perianth united for up to half their length, greenish-white or pink. Fruit 1·5–2·5 mm, dull, but sometimes shining on the edges, with two convex and one narrowly concave sides, (rarely with two sides concave and one convex), or sometimes biconvex, brown to black, not or only a little exserted from the persistent perianth. Flowers July to November.

Holotype not traced (but see later).

The taxonomy of these two species is best considered together both from the point of view of nomenclature and their geographical distribution.

The nomenclatural problems of the two species are most involved. In splitting the Linnean *P. aviculare*, Lindman (1912), according to the *International Code of Botanical Nomenclature*, should have kept the latter binomial for one of his segregated species. Instead, however, he published two new names, *P. heterophyllum* and *P. aequale*, giving *P. aviculare* L. *pro parte* under both. In trying to equate *P. aviculare* with one of these names in order to conform with the accepted rules, some authors (Komarov 1936, Lembke 1948, Chrtek 1956 and A. & D. Löve 1956) have given the name *P. aviculare* to *P. aequale*, whereas others (Moss 1914, Tutin 1952, Dandy 1958 and Rechinger (in Hegi 1958)) have given it to *P. heterophyllum*. Those authors who take *P. aequale* Lindm. to be *P. aviculare* L., retain *P. heterophyllum* as the name for the other species. This name, however, is illegitimate since Lindman himself includes under it subsp. *rurivagum* based on the earlier *P. rurivagum* Jordan ex Boreau. A. & D. Löve and Chrtek give no reasons for retaining *P. aviculare* L. as the correct name for *P. arenastrum*.

In the Linnean herbarium under *P. aviculare* there are 5 specimens but only one bears the name *P. aviculare* in Linnaeus' handwriting. It is a large leaved heterophyllous plant with fruit *c.* 3 mm and a persistent perianth with segments divided almost to the base. This is *P. heterophyllum* Lindm. and the Linnean name must therefore stand for it. The specimen falls well within the range of variation of British and west-European plants that I call *P. aviculare, sensu stricto*. Since the phrase-name in *Hortus Cliffortianus* is not cited by Linnaeus in *Species Plantarum*, this specimen may be regarded as the type. It seems better to retain this well-known name since it has been used correctly by many British and European botanists. *P. monspeliense* is the correct name if *P. aviculare* is rejected, since *P. centinodium* is illegitimate.

The name *P. aequale* Lindm. cannot be retained because earlier names are available. I have obtained specimens of *P. aviculare, sensu lato*, from Boreau's herbarium at Angers, but unfortunately there is no specimen here which can be taken as the type of his *P. arenastrum*. Plants however, collected and labelled as this (in what is taken to be Boreau's handwriting) at a date later than 1857 fall very well into the range of variation exhibited by British plants. There thus seems no doubt of Boreau's intentions as all specimens labelled *P. arenastrum* in his herbarium belong to the same species. I propose therefore to use this name, *P. arenastrum* Bor., for the taxon usually called *P. aequale* Lindm. *P. arenastrum* was frequently used by botanists in this country prior to the publication of the name *P. aequale* by Lindman either as a specific name or as a variety of *P. aviculare*.

Although the names *P. arenastrum* and *P. microspermum* were published at the same time by Boreau (1857) I retain the former in that it refers to plants with broader leaves which are the commoner form. The two names have not been combined previously so far as I am able to discover.

Scholz (1959) rejects the name *P. aviculare* L. on the grounds that it is a *nomen ambiguum* and replaces *P. heterophyllum* by *P. monspeliense*. As already mentioned, the latter is, in fact, the correct name for this species if *P. aviculare* is not used. As I have

been able to typify the Linnean species, there is no reason why the name should not be retained.

I do not at the present time propose to recognize any infraspecific categories within the two taxa. As is well known in plants where a high degree of inbreeding is prevalent, homogeneous populations occur which differ only slightly from other populations. This has often led to the description of numerous meaningless microspecies in *Polygonum* as in other common weed species. Both *P. aviculare* and *P. arenastrum* are very polymorphic and are markedly affected by habitat conditions. They also show great genetic plasticity in all their morphological characters. Until more controlled breeding experiments can be carried out it is perhaps best to consider them as two variable groups with the status of species in the 'Linnean' sense.

Ecotypic forms of *P. arenastrum* are recognizable and these show a certain degree of constancy in habitats of the same type. These showed some morphological differences when their offspring were raised in the experimental garden.

I have found that *P. calcatum* Lindm. cannot be maintained as a distinct taxon in this country at least. The differences between it and *P. aequale* are not clearly stated by Lindman (1904, 1912) and those attributed to it by Moss (1914) and other authors have not been found sufficiently constant to warrant its maintenance as a species or even subspecies (see p. 196 above and Table 7). Professor H. Nannfeldt of Uppsala (*in litt.*) states that in Sweden also many botanists agree that this plant is not a distinct species.

It is also suggested that *P. microspermum* Jord. is not a distinct taxon. Measurements of a small number of plants named by Jordan as this have been obtained from several European herbaria. These plants were analysed but were found to be inseparable from forms of *P. arenastrum*. In this country narrow-leaved plants with small fruits have been given this name. Small-fruited forms are biometrically inseparable from the overall variation pattern of this character in *P. arenastrum* (see Table 9).

A study of the type of Besser's *P. neglectum* from Kiev (**KW**) shows that it is a different form from any met with in west Europe. The specimen is a poor one but agrees fairly well with the figure given by Lembke (1948) from Polish specimens. It has proved impossible to obtain an idea of the morphological range of this species owing to its being very poorly represented in European herbaria, and hopelessly confused in the literature. It is probable that it has a more easterly distribution and could have been introduced into Canada.

Geographical Distribution

British Isles

Both species are very common as weeds throughout the whole of this country. Druce (1932) records *P. aviculare, sensu lato*, for every vice-county in Great Britain, mentioning that the common plant is *P. heterophyllum* Lindm.

I have seen specimens of both species in British herbaria from every vice-county; I have also received many records besides from the BSBI Distribution Maps Scheme.

It is clear that the two species have different ecological preferences. The estimated percentages in Table 13 must be regarded as only a very rough guide since not all habitats fall clearly into any of the categories listed. These results were obtained from data compiled during my field work on approximately 200 habitats in Great Britain. The two species are often found growing together forming mixed populations. *P. aviculare* occurs most commonly in cultivated areas, cornfields, etc. (87%), whereas *P. arenastrum* tends to be found at the edges of fields, in bare patches, and on paths and roadsides (82%). It is on the whole a smaller plant, and most frequently prostrate, which seems to account for the ecological differences. *P. arenastrum* appears to be able to tolerate a greater amount of treading and trampling than *P. aviculare*. The former has been observed on footpaths which were trampled on daily by human beings and farm animals, but the plants were not eliminated. In maritime areas, I have noticed too that the two species occur in about the same frequency, but again *P. arenastrum* survives in places where trampling is most severe.

TABLE 13.
Ecological preferences of *P. aviculare* and *P. arenastrum*.

Habitat	P. aviculare	P. arenastrum
Cornfields	66%	10%
Other cultivated fields e.g. potato fields, *Brassica* crops, legumes	21%	34%
Tracks and roadsides (pavements, metalled streets, footpaths)	1%	36%
Waste ground (farmyards, building sites, etc.)	4%	12%
Maritime habitats	6%	6%
Other habitats (gardens, etc.)	2%	2%

On the whole the latter species thrives in drier situations than *P. aviculare*, as on gravel drives, roadsides, pavements and tracks.

Foreign Distribution

P. aviculare agg. has a world-wide distribution except for the Antarctic, and it is presumed that the two species *P. aviculare* and *P. arenastrum* have similar geographical distributions though with some ecological differences. I have seen herbarium specimens of both from most European countries and there are records for many parts of Asia. *P. plebejum* is, however, said to replace *P. aviculare* in some parts of India, Ceylon and parts of Africa. *P. aviculare* and *P. arenastrum* are now well established in N. America, but detailed information on their occurrence in S. America and Australasia is lacking.

3. P. RURIVAGUM Jord. ex Bor., Fl. Centre de la France, Ed. 3, **2**: 560 (1857).

P. aviculare var. *rurivagum* (Jord. ex Bor.) Gentil, Inv. pl. Sarthe, 218 (1892).

P. heterophyllum subsp. *rurivagum* (Jord. ex Bor.) Lindm., Svensk Bot. Tidskr. **6**: 691 (1912).

Annual. Plant very slender, flexuous, suberect, seldom more than 30 cm, heterophyllous. Leaves linear-lanceolate to linear, acute, 1·5–3·5 cm long and 0·5–1·4 mm wide. Ochreae brownish-red below, *c.* 10 mm long, longer than in related species. Inflorescence 1-2-flowered, seldom more. Perianth segments narrow, shorter than *P. aviculare*, reddish, not overlapping. Fruit 2·5–3·5 mm × 1·5–2 mm, exserted from the persistent perianth, with 3 concave sides, scarcely shining. Fruit as long as, but narrower than that of *P. aviculare*. Flowers from August to November.

Holotype not seen (but see below).

There are no Jordan specimens of *P. rurivagum* in the Boreau herbarium, but there are others, the collector of which is unknown (the handwriting is evidently not that of Jordan). I have, however, seen three specimens of the latter from his own collections at Lyon gathered by himself in 1860. This is three years after the publication of Boreau's *Flore du Centre de la France* (Ed. 3). As the specimens in the two herbaria are the same plant I propose to keep the name *P. rurivagum* for this species.

Geographical Distribution

British Isles

This species is not well known, and is probably overlooked in Great Britain. Its distribution needs further investigation. I experienced considerable difficulty in tracing populations of this plant and have found very few records of it.

P. rurivagum occurs most frequently in cornfields and cultivated places, and so far as is known, only on chalky or other light soils. All my records are from the south and south-west of England. It is easily recognizable from *P. aviculare*, with which it sometimes grows, by its slender and flexuous habit, very narrow acute leaves and long reddish brown ochreae.

I have gathered material myself from vice-countries 8, 13, 14, 22 and 29, and further localities have been provided by the BSBI Plant Distribution Maps Scheme or herbarium specimens from v.c. 7, 9, 11, 16, 17, 18, 24, 30, 31, 54 and 58. There are specimens from all of these except 54 and 58 where the determinations must remain doubtful.

Moss (1914) gives the plant's further distribution as Leicestershire, Durham, Dumbarton and Perthshire. These records again need confirmation.

Foreign Distribution

The species was first recorded from France by Jordan. I have seen many French specimens and there are duplicates of these in the herbarium at Munich (**M**). It will probably prove much more common with further searching and will no doubt be found to occur in most western European countries.

As stated above, A. & D. Löve record *P. rurivagum* from Canada with the diploid chromosome number ($2n = 20$). The achenes of this plant are stated to be small, from 1–1·5 (rarely up to 2 mm) long, whilst British plants of this species have fruits which are as long as in *P. aviculare* but narrower. I have sent British specimens of this species to Professor A. Löve for examination and he agrees that they differ from the Canadian plants to which he gives this name.

4. P. BOREALE (Lge.) Small, Bull. Torr. Bot. Club **21**: 479 (1894).

P. aviculare var. *boreale* Lge., Medd. om Groenl. **3**: 105 (1880).

[*P. islandicum* Meisn. ex Small, Mem. Dept. Bot. Columbia Coll. **1**: 108, et tab. 41. (1895) nom. illegit.].

P. heterophyllum var *boreale* (Lge.) Lindm., Svensk Bot. Tidskr. **6**: 691 (1912).

P. heterophyllum subsp. *boreale* (Lge.) A. & D. Löve, Acta Hort. Gotoburgensis **20**: 216 (1956).

Annual. Plant up to 100 cm, erect or suberect, simple or sparingly branched, markedly heterophyllous. Stem leaves oblong-obovate to spathulate, the lower blades 3–5 cm long and 0·5–1·8 cm broad; petioles 4–8 mm, projecting from the ochreae. Ochreae 5–8 mm, silvery or brownish, only slightly lacerate. Flowers large, *c.* 4–5 mm. Petaloid margins of perianth segments broader than those of *P. aviculare* L., pinkish or white. Segments inclined to open in fruit, longer than in the other species, *c.* 2·5–3·0 mm. Fruit triquetrous, punctate, dull, light or dark brown, 3·5–4·5 mm × *c.* 2·5 mm broad, with 3 broadly concave sides (sometimes 4), included, or with the apex just protruding from the lax perianth segments. Flowers June to October.

This species has the largest fruit yet observed in plants of the *Polygonum aviculare* aggregate, and has flowers approaching *P. raii* and *P. maritimum* in size.

Holotype, Botanical Museum, Copenhagen, Denmark (**C**) Legit J. Lange, Greenland, 1880.

Geographical Distribution

British Isles

This species is new to the British Isles, although Druce (1912) used the name *P. aviculare* var. *boreale* for plants gathered at Loch Leven, Fife (v.c. 85). There was, however, at the time great confusion between this variety and the plant then known as *P. littorale*. It is at present only known from the Shetlands and Orkney Islands. Druce (1922) records a forma *grandiflora* [*sic*] of *P. aviculare* var. *littorale* from Uyea Sound, Shetland, and it was from a study of this specimen and others in the Druce Herbarium, Oxford, that I decided to investigate the Shetland populations further.

Foreign Distribution

I have seen harbarium specimens of this species from Iceland, Faroes, Greenland and Northern Scandinavia.

A. & D. Löve's records for northern Canada need to be checked but may well be correct, since the description of the Canadian plants studied agrees with European and Greenland plants but differs from their earlier description of plants from Iceland.

Small (1894), after raising Lange's variety *boreale* of *P. aviculare* to full specific rank, published the name *P. islandicum* in 1895. It is apparent that after having published the first of the binomials he received a sheet of *P. boreale* from De Candolle's herbarium at Geneva collected from Iceland in 1866 by M. E. Jardin labelled by Meisner as *P. islandicum* The latter author, however, never published this name and it is therefore not valid. The name *P. boreale* (Lge.) Small must be retained for this species. Further work is needed to establish the extent of the distribution of *P. boreale* in northern Scotland.

5. P. RAII Bab., Trans. Linn. Soc. Lond. **17**: 458–9 (1836).

P. dubium Deakin, Florig. Brit. **2**: 576 et tab. 656 (1845), nom. illegit.

P. maritimum β *raii* (Bab.) Lloyd, Fl. Ouest France, ed. **2**: 430 (1868).

[*P. littorale sensu* Gren. & Godr., Fl. de France **3**: 51–2 (1855), non Link].

P. raii subsp. *norvegicum* Sam., Acta Hort Bergiani **11**: 72 (1931).

[*P. robertii* auct.].

Annual. Plant prostrate, glabrous, sometimes glaucous and slightly fleshy, 10–100 cm. Stems more or less woody at the base. Leaves 1–3·5 cm, elliptic-lanceolate to linear-lanceolate, usually flat, though the young ones sometimes appear revolute. Ochreae shorter than upper internodes, laciniate, *c.* 5 mm, hyaline and silvery in the upper part with 3–6 unbranched veins. Inflorescence 2–6-flowered. Flowers large, pink or white. Perianth segments *c.* 3 mm, with broad petaloid margins. Stamens 8. Fruit 5–6 mm long × 3–3·5 mm broad, light brown, flattened, smooth, shining, much exceeding the persistent perianth. Flowers from June to September.

Holotype in the University Herbarium, Cambridge (**CGE**). Legit Borrer. Sands between Marazion and Penzance, Cornwall, 1836.

Geographical Distribution

British Isles

P. raii is an interesting Atlantic species which formerly occurred fairly frequently on sands and shingle in maritime areas just above the high tide mark around the coasts of Britain (see Fig. 11).

Associated species growing with *P. raii* at Freshwater Bay, Pembrokeshire (v.c. 45) were *Euphorbia paralias*, *E. portlandica*, *Salsola kali*, *Cakile maritima*, *Ammophila arenaria* and *Chenopodium* spp.

From records received by the BSBI Distribution Maps Scheme there is evidence that it is decreasing in frequency in this country. I have searched for it, without success, in many of the localities in Wales and in the west and south of England where it has been recorded in the literature as common. The plant was very local in two areas (Hayling Island, S. Hants (v.c. 11), and Maenporth, Cornwall (v.c. 1)). It was formerly common locally along the coasts of south England, Wales, west Scotland and the Hebrides and on the east from Durham to Angus. It has been recorded from nearly all the coastal counties in Ireland. Druce gives the following vice-county records of the species in the British Isles.

S, 1–6, 9–11, 13–16, 18, 34, 37, 41, 44–46, 48–52, 53, 54, 58–60, 66–76, 82, 83, 85, 87, 90, 97–99, 100–104, 110 H, 1–3, 5–6, 9, 12, 15–16, 20–22, 27, 31, 34, 35, 38–40.

I have added the plant new to v.c. 106, where it was recorded by Marshall at Ballintore, E. Ross in 1910, but named by him *P. aviculare* var. *littorale* Link (**BM**). I have seen specimens from all the above vice-counties except 34, 37, 53 and 54. The last two records are suspect. Vice-county 37 is inland (Worcs.), but the occurrence of *P. raii* is possible since the river Severn is tidal along its lower reaches.

Foreign Distribution

Moss (1914) gives the extra-British distribution of *P. raii* as southern Scandinavia, Denmark, Germany, Belgium, France, northern Russia, Spain, Italy and the west coast of North America. Specimens are extant from the following; north-west France, Belgium, north Germany (Heligoland) (Scholz 1957), Norway and Denmark. Dr. Bengt Pettersson tells me (*in litt.*) that *P. raii* does not occur in Sweden where it is replaced by *P. oxyspermum*. Specimens tentatively named *R. raii* from Portugal by Dr. A. R. Pinto da Silva were *P. maritimum* (atypical). I have been unable to trace specimens or records for Spain and Italy, and, as the species appears to have an exclusively Atlantic distribution, I regard them as having been based on misidentified material.

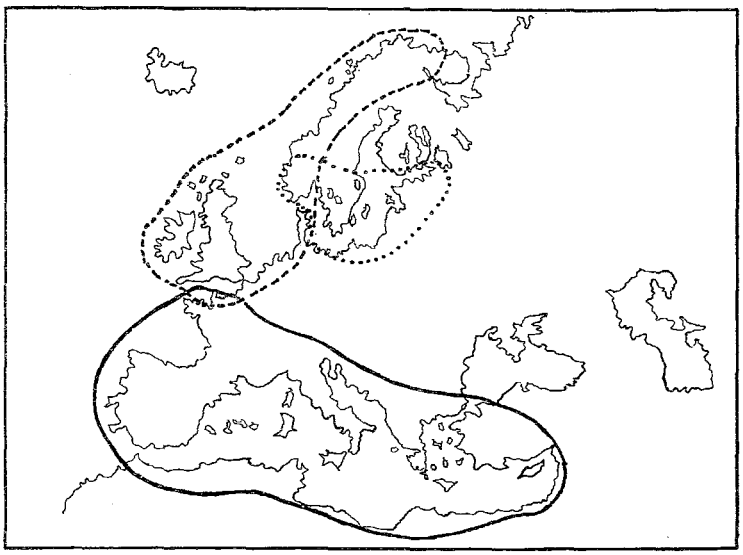


Fig. 11. Distribution in Europe of *P. maritimum* (solid line), *P. raii* (dashes) and *P. oxyspermum* (dots).

P. raii is recorded from northern Russia by Komarov (1936). The name *P. raii* is given in certain east-European Floras, Savălescu (1952), Stoyanoff & Stefanoff (1933) for plants collected around the Black Sea. I have seen specimens named *P. raii* from this area. They are morphologically very close to west-European plants to which I give this name and I am investigating them further. Chrtek (1960) has described two new species in the group from this area. One of these also seems to be very close to *P. raii*.

The north American records present a problem. Many recent Floras and Manuals of selected areas of this continent, *e.g.* Fernald (1950), Gleason (1952) and Roland (1947), give accounts of it but it appears that it may be a different cytological race. I have seen specimens in the Kew herbarium (**K**) which are undoubtedly *P. raii*.

I can find no basis for retaining Samuelsson's subspecies *norvegicum* (1931) of *P. raii*. The differences attributed to it are small. It differs from the type in having more flowers in the inflorescence and narrower non-overlapping perianth segments with a broad white edge. All of these characters are most variable and are not of great taxonomic significance within the section. Both pink and white flowers occur in plants of *P. raii* from Great Britain. Plants from Norway have been called exclusively subspecies *norvegicum*.

Many British, Continental and American botanists during the latter half of the last century named plants belonging under *P. raii* Bab. as *P. robertii* Lois. The confusion arose in this country in the first instance because no British botanists had seen authentic material of the latter, while Meisner (in De Candolle 1856) states that material sent to him by Loiseleur-Deslongchamps was a mixture of *P. raii*, *P. littorale* and *P. aviculare* and that the name ought to be completely abolished. Loiseleur's species was described from maritime sands of the Mediteranean, and since *P. raii*, according to Rouy (1910), does not occur south of the shores of the English Channel, it is hardly probable that the plant collected by Robert on the sands near Toulon is identical with the northern one. Furthermore, Rouy maintains *P. robertii* is a very distinct plant of the Mediterranean sands with shining achenes 2–3 mm long. Under these circumstances it is correct to keep the name *P. raii* for Babington's plant, and no change in the binomial is proposed.

6. P. OXYSPERMUM Mey. & Bge., in Ledebour, Ind. Sem. Hort. Acad. Dorpat. Suppl. **2**: 5 (1824).

P. acadiense Fernald, Rhodora **16**: 188 (1914).

After examining a number of specimens of *P. oxyspermum* from Denmark, Sweden and Scotland, I feel that the status of this plant as a full species is doubtful. Many of the differences given by Samuelsson are based on characters which show great variability. Although I was able to detect the colour differences of the achenes and perianth on plants collected in 1957, I found this impossible in older specimens. The narrowness of the fruit is an important feature, but I was unable to separate *P. raii* from it on this character alone.

Although *P. oxyspermum* has a Baltic distribution (neglecting Canadian records) there is considerable overlap of this species with *P. raii* in southern Scandinavia and Denmark (Fig. 12). Before any taxonomic conclusion can be made on the distinctness of these two species more information is required on their behaviour in these areas of overlap. There is a chance of hybridization since the plants occupy similar types of habitat, the flowers are larger and more attractive than those of *P. aviculare, sensu lato* and the European populations have the same chromosome number.

I think that *P. oxyspermum* and *P. raii* may be better treated as geographical subspecies of one species, but until more information is forthcoming on the facts mentioned above the question must remain unanswered. The two are being grown under experimental conditions and I hope to publish a fuller account of these two species later.

There are several specimens in Herb. Mus. Brit. which have been labelled by Samuelsson as *P. oxyspermum*, although the original collectors identified them as *P. raii*. The localities are: Gosfort, Haddington 1850 (v.c. 82); Mornfar, Forfar, 1845 (v.c. 90); Carnoustie, Angus, 1845 (v.c. 90); Musselburgh, W. Lothian, 1842 (v.c. 83).

There is also another, originally named as *P. aviculare* var. *littorale*, collected from a salt marsh, Warrenly, Yorks., v.c. 62, which is also called ? *P. oxyspermum* by Samuelsson.

I have studied these specimens, but at the moment feel uncertain about their correct determination. They are all old and the colour and narrowness of the fruit is not evident. The Carnoustie plant (the same form was also obtained from Dundee), did not have red borders to the flowers, which is given as diagnostic for the species by Samuelsson (1931), and I could not see that the perianth segments were any narrower than in specimens of *P. raii*. There are no very evident differences in leaf morphology and internode length, which are very variable characters in the group.

7. P. MARITIMUM L., Sp. Pl. 361 (1753).

P. maritimum var. *confusum* Rouy, Fl. France **12**: 110 (1910).

A glabrous, glaucous, prostrate or erect shrubby (in south Europe) perennial, 10–50 cm; root stock woody and stout at the base. Leaves 0·5–2·5 cm, elliptic-lanceolate, greyish-green, margins usually revolute. Ochreae very conspicuous and silvery-white above, usually

longer than the upper internodes which they envelop, 2-lobed at first but eventually becoming lacerate, with 6–12 strong branched veins. Inflorescence 1–4-flowered. Flowers twice as large as those of *P. aviculare*. Perianth segments *c.* 2–2·5 mm, with pink or white broad petaloid margins. Stamens 8. Fruit 4–4·5 mm long × *c.* 2·5 mm broad, ovoid, acute, reddish chestnut-brown, smooth, shining, as long as or slightly exceeding the persistent perianth. Flowers July to September.

Holotype in Linnean Herbarium (**LINN**), London.

Geographical Distribution

The British Isles

This species is now thought to be extinct on the mainland of Great Britain, since no plants have been found since about 1939 (coll. C. West nr. Mullion, Cornwall, v.c. 1) in spite of the increased activities of the members of the BSBI engaged in the Maps Scheme. The well known colony of approximately 30 plants was seen on Herm, Channel Islands in 1961. They were growing in bare unstable coarse shell-sand just above the high tide mark with *Beta vulgaris* subsp. *maritima*, *Carex arenaria* and *Brachythecium albicans* as associate species.

Although never very abundant in any one locality in this country, I have seen herbarium specimens from the following vice-counties in the south of England :

S. (Guernsey, Herm) 1 (including Scilly Isles), 2–5, 6, 9, 11.

Druce also gives the following v.c. records in brackets : 13, 28, 46, 49, 75. All are suspect and no specimens are available for their confirmation.

P. maritimum is a Mediterranean species which reaches its northernmost limits in Great Britain. As in many other plants at the edge of their geographical range, the British specimens are not quite typical and differ in certain characters from the main body of the Continental material. The Herm plants are more herbaceous than those obtained from Sacavém, Portugal and Banyuls, Pyr.-or., France and have shorter ochreae with less conspicuous veins. The British populations on Herm (*fide* Mrs. F. Le Sueur) behave as perennials but other specimens seen from Braunton Burrows suggest from their herbaceous appearance that the plant might have behaved as an annual on the mainland.

It is quite possible that fruits of *P. maritimum* could be carried by ocean currents and thereby washed up on to the shore by tides. I have no doubt that the plant could become established again in the south and west of England given the right conditions.

Foreign Distribution

P. maritimum occurs frequently on sandy shores and shingle in the following European areas from which I have seen specimens : western (Manche) and southern France, Iberian Peninsula, Macaronesia, Mediterranean Europe, Corsica; also in Asia Minor and north Africa. Moss (1914) gives the following further records, Cape Colony, South Africa (rare), North America (Massachusetts to Florida) and South America. I have seen no specimens nor can I trace records from the first and last continents mentioned, and consider the occurrence of the plant here most doubtful. The North American records are, according to Fernald (1913), all based on wrongly identified material. Linnaeus (1753) includes American plants with his frutescent Mediterranean species *P. maritimum*, saying 'Habitat Monspelii, in Italia, Virginia, [perennial].' Several American authors, Pursh (1814), Torrey (1843) and Small (1895), have included *P. maritimum* in their Floras and Manuals but it is now fairly certain that the American plant referred to by Linnaeus is in fact *P. glaucum* Nutt. This species is an American endemic and differs from *P. maritimum* in that it is always annual and herbaceous, with shorter ochreae, 7–10 mm, and in the fruits, which are distinctly smaller, 3–4 mm long and 1·6–2·2 mm wide. It is very probable that Linnaeus included his American plants of this species under *P. maritimum*. There is still much confusion in American floras over the maritime species in this section and experimental work on their taxonomy is urgently needed.

ARTIFICIAL KEY TO THE BRITISH SPECIES*

1. Fruit dull, striate, enclosed by or slightly longer than the persistent perianth. *3*
   Fruit smooth, distinctly shining, as long as or longer than the persistent perianth. *2*
2. Ochreae with 4–6 unbranched veins, shorter than the upper internodes; fruit 5–6 mm long, exceeding persistent perianth. 5. *raii* †
   Ochreae with 8–12 branched veins, as long as upper internodes; fruit 4–4·5 mm long, enclosed by or slightly projecting from persistent perianth (very rare). 7. *maritimum*
3. Branch leaves much smaller than stem leaves; persistent perianth divided almost to base; fruit trigonous, with 3 concave sides. *4*
   Branch and stem leaves ± equal; persistent perianth divided for half its length; fruit with 2 sides convex, one concave. 2. *arenastrum*
4. Stem leaves narrow, linear-lanceolate, 1–4 mm broad; perianth segments and fruit narrow. 3. *rurivagum*
   Stem leaves 5–18 mm broad; perianth segments overlapping; fruit broad. *5*
5. Stem leaves ovate-lanceolate, subsessile or with petioles *c.* 2 mm included in the ochreae; fruit 2·5–3·5 mm long. 1. *aviculare*
   Stem leaves obovate-spathulate; petioles 4–8 mm, projecting from ochreae; fruit 3·5–4·5 mm long (Shetland). 4. *boreale*

ACKNOWLEDGMENTS

My grateful thanks are due to Dr. E. F. Warburg for his help and guidance during the progress of this work and for his careful criticism of the manuscript. Also to Dr. K. R. Lewis for help with the cytological problems involved, and to numerous correspondents who have lent or given me specimens.

REFERENCES

ANDERSON, E. (1949). *Introgressive Hybridization.* New York.
ANDERSSON, E. (1942) in A. & D. Löve (1942a).
ANDERSSON, E. (1948) in A. & D. Löve (1948).
ASCHERSON, P. & GRAEBNER, P. (1913). *Synopsis der Mitteleuropäischen Flora*, **4**. Leipzig.
BABINGTON, C. C. (1836). On several new or incompletely understood British and European plants. *Trans. Linn. Soc. Lond.*, **17**, 451–464.
BESSER, W. (1822). *Enumeratio plantarum hucusque in Volhynia, Podolia, Gub. Kiioviensi, Bessarabia Cis-Tyraica et circa Odessam collectarum*, etc. Vilna.
BOREAU, A. (1857). *Flore du Centre de la France*, **2**, Ed. 3. Paris
CHRTEK, J. (1956). Proměnlivost druhu *Polygonum aviculare* L. v Č.S.R. *Preslia*, **28**, 362–368.
CHRTEK, J. (1960). Neue Arten der Gattung *Polygonum* L. *s. str. Preslia*, **32**, 366–368.
DANDY, J. E. (1958). *List of British Vascular Plants.* London.
DARLINGTON, C. D. & LA COUR, L. F. (1947). *The Handling of Chromosomes.* Ed. 2. London.
DE CANDOLLE, A. -P. & LAMARCK, J. B. (1815). *Flore Française*, **3**. Ed. 3. Paris.
DRUCE, G. C. (1922). *Flora Zetlandica.* Arbroath.
DRUCE, G. C. (1932). *The Comital Flora of the British Isles.* Arbroath.
FERNALD, M. L. (1913). Some N. American relatives of *Polygonum maritimum. Rhodora*, **15**, 68–72.
FERNALD, M. L. (1914). A new maritime *Polygonum* from Nova Scotia. *Rhodora*, **16**, 187–189.
FERNALD, M. L. (1952). *Gray's Manual of Botany.* Ed. 7. New York.
GLEASON, H. A. (1952). *The New Britton and Brown, Illustrated Flora of the Northeastern United States and Adjacent Canada*, **2**, Lancaster, Pa.
HESLOP-HARRISON, J. (1952). Statistical methods in plant taxonomy. *Taxon*, **1**, 53–59, 73–78.
International Code of Botanical Nomenclature, 1956. Utrecht.
JARETZKY, R. (1928). Histologische und Karyologische Studien an Polygonaceen. *Jahrb. wiss. Botan.* **69**, 357–490.
JUSTICE, O. L. (1941). A study of dormancy in seeds of *Polygonum. Mem. Cornell Agric. Expt. Stat.* 235–243.
KOCH, W. D. J. (1837). *Synopsis Florae Germanicae et Helveticae* etc., **2**, Ed. 1. Frankfurt a/M.
KOMAROV, V. L. (1936). *Flora U.R.S.S.*, **5**, Leningrad–Moscow.

*Identifiable with certainty only if ripe fruit and stem leaves at least at 2nd or 3rd node are present.
† see also 6. *oxysperum*

LANGE, J. (1880). Conspectus Florae Groenlandicae. *Medd. om Grönl.*, **3**, 1–214.
LEDEBOUR, C. F. (1850). *Flora Rossica*, **3**, Stuttgart.
LEMBKE, J. (1948). Étude sur les menues espèces appartenant à l'espèce collective *Polygonum aviculare* L. *Acta Soc. Bot. Polon.* **19**, 201–207.
LINDMAN, C. A. M. (1896). *Polygonum aviculare* L. f. *littoralis* (Link) i Skandinavien. *Bot. Not.* 75–80.
LINDMAN, C. A. M. (1904). *Polygonum calcatum* nov. spec. inter *Avicularia. Bot. Not.* 139–147.
LINDMAN, C. A. M. (1912). Wie ist die Kollectivart *Polygonum aviculare* zu spalten? *Svensk Bot. Tidskr.* **6**, 673–696.
LINK, H. F. (1821). *Enumeratio Plantarum Horti Regii Botanici Berolinensis altera*, **1**, Berlin.
LINNAEUS, C. (1753). *Species Plantarum*. Stockholm.
LOISELEUR-DESLONGSCHAMPS, M. J. L. (1827). Nouvelle notice à ajouter à la Flore de France. *Mém. Soc. Linn. Paris*, **6**, 1–40.
LÖVE, A. & D. (1942a). Chromosome numbers of Scandinavian Plant Species. *Bot. Not.* 19–59.
LÖVE, A. & D. (1942b). Cytotaxonomic studies on boreal plants I. Some observations on Swedish & Icelandic plants. *Kgl. Fysiograf. Sällskap. Lund Förh*, **12**, 1–19.
LÖVE, A. & D. (1948). Chromosome numbers of Northern Plant Species. *Iceland Univ. Inst. App. Sci. Dept. Agric. Rep.* B, **3**, 1–131.
LÖVE, A. & D. (1956a). Cytotaxonomic conspectus of the Icelandic Flora. *Acta Horti Gotoburgensis* **20**, 65–290.
LÖVE, A. & D. (1956b). Chromosomes and taxonomy of eastern N. American *Polygonum*. *Canad. Journ. Bot.* **34**, 501–521.
MEISNER, C. F. (1826). *Monographiae Generis Polygoni Prodromus*. Geneva.
MEISNER, C. F. (1856). *Polygonaceae* in A.-P. De Candolle, *Prodromus Systematis Naturalis* **14**. Paris.
MEYER, C. A. & BUNGE, D. A. (1824), in Ledebour, C. F. *Indicis Seminum Horti Academici Dorpatensis*. Supplementum 2. Dorpat.
MOSS, C. E. (1914). *The Cambridge British Flora* **2**, Cambridge.
OSTENFELD, C. H. (1916), in Fernald, M. L. On the occurrence of *Polygonum acadiense* in Denmark. *Bot. Tidsskr.* **34**, 253–255.
PAUVELS, L. (1959). Études critiques sur quelques *Polygonum* de Belgique. *Bull. Soc. Roy. Bot. Belg.* **91**, 291–297.
PERSOON, C. H. (1805). *Synopsis Plantarum* etc. **1**, Paris.
PÓLYA, L. (1948). Chromosome numbers of certain alkali plants. *Arch. Biol. Hung. Ser. II.* **18**, 145–148.
PURSH, F. (1814). *Florae Americae Septentrionalis* **1**, London.
RECHINGER, K. H. (1958). *Hegi's Illustrierte Flora von Mitteleuropa* **3**, Ed. 2. München.
REYNIER, A. (1905). Notes sur les plantes distribuées. *Bull. Herb. Boiss.* **5**, 980–983.
ROLAND, A. G. (1947). The Flora of Nova Scotia. *Proc. Nova Scotian Inst. Sc.* **21**, **3**, 95–642.
ROUY, G. (1910). *Flore de France* **16**. Paris.
SAMUELSSON, G. (1931). *Polygonum oxyspermum* Mey. et Bge. und *P. raii* Bab. ssp. *norvegicum* Sam. n. ssp. *Acta Horti Bergiani* **11**, 67–80.
SAVĂLESCU, T. (1952). *Flora Republicii Populare Romîne* **1**, Bucharest.
SCHOLZ, H. (1957). Über ein Vorkommen des Strandknöterichs *Polygonum raii* in Deutschland. *Ber. Dtsch. Bot. Ges.* **70**, 484–488.
SCHOLZ, H. (1958–9). Die Systematik des europäischen *Polygonum aviculare* L. I, *Ber. Dtsch. Bot. Ges.* **71**, 427–434; II *ibid.* **72**, 63–72.
SCHOLZ, H. (1960). Bestimmungsschlüssel für die Sammelart *Polygonum aviculare* L. *Verh. Bot. Prov. Brand.* **98–100**, 180–182.
SCHRADER, J. (1800). *Journal für die Botanik* **1**, 1. Göttingen.
SMALL, J. K. (1894). Some notes on the rarer species of *Polygonum*, *Bull. Torr. Bot. Club* **21**, 476–482.
SMALL, J. K. (1895). Monograph of the N. American species of the genus *Polygonum*. *Mem. Dept. Bot. Columbia College* **1**, 1–183.
STOYANOFF, N. & STEFANOFF, B. (1933). *Flora of Bulgaria*, Ed. 2. Sofia.
STYLES, B. T. (1960). The Taxonomy of the British Knotgrasses, in *The Biology of Weeds. British Ecological Society Symposium* No. 1, 48–54.
TORREY, J. (1843). *Flora of New York State* **2**. New York.
TUTIN, T. G. (1952), in Clapham, A. R., Tutin, T. G. & Warburg, E. F., *Flora of the British Isles*. Ed. 1. Cambridge.
WARBURG, E. F. (1960). Some taxonomic problems in weedy species, in *The Biology of weeds. British Ecological Society Symposium* No. 1, 43–47.