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TAXONOMIC STUDIES IN THE ALSINOIDEAE: I. GENERIC AND INFRA-GENERIC GROUPS

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This is the first of two papers embodying the main conclusions of a thesis accepted for the degree of Ph.D. by the University of Edinburgh (McNeill, 1960a). The thesis dealt with the *Arenaria* group of genera and fell into two parts: in the one a general examination was made of generic and infra-generic limits on a world basis, while the other represented the results of a complete revision of the species occurring in the Orient. Descriptions of nine new species of *Arenaria* and *Minuartia* from this area have already been published (McNeill, 1961).

This present account covers the generic and infra-generic revision; the full revision of Orient species will be published in the succeeding paper. Discussion of evolutionary trends, enumeration of chromosome numbers and citation of specimens examined, all forming extensive parts of the thesis, are being omitted from these extracts for publication.

During a two month visit to Turkey in 1956 (as botanist on the Oxford Expedition to South Eastern Turkey), the author was able to observe and make collections from a wide range of habitats in both the Mediterranean and Irano-Turanian vegetation regions. A number of species of the group were found growing in the wild and the insight thus gained into their phytogeography and ecology has been of great value in the present studies.

The taxonomic revisions have been based chiefly on the collections in the Herbaria of the Royal Botanic Garden, Edinburgh and the Royal Botanic Gardens, Kew. Visits have also been made to the Herbaria at the British Museum (Natural History), the Linnean Society, the Manchester Museum and the Department of Botany, University of Oxford. For the revision of the Orient species valuable type material has been borrowed from the Conservatoire et Jardin Botaniques, Geneva, the Museum National d'Histoire Naturelle, Paris and the Instituto Botanico dell'Universita, Turin, while the entire Orient collections of the following

Herbaria have been examined: Institut für Spezielle Botanik und Herbarium Haussknecht, Jena; Institutum Botanicum Universitatis Carolinae, Prague (*Minuartia* only); Naturhistoriska Riksmuseum, Stockholm; Naturhistorisches Museum, Vienna; and Botanische Institut und Botanischer Garten der Universität, Vienna.

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INTRODUCTION

The members of the sub-family *Alsinoideae* are distinguished from the *Silenoideae* by their free sepals, and from the *Paronychioideae* (including *Spergulineae* and *Illecebraceae*) by their exstipulate leaves and by possessing true petals (not petaloid staminodes).

The present studies have been confined to the free-styled capsular members of the sub-family, that is to the sub-tribes *Stellariinae* and *Sabulininae* of Pax and Hoffmann (1934, pp. 295-296) as amended by Mattfeld (1934, p. 367). These sub-tribes are regarded in the "Pflanzenfamilien" as comprising 11 and 10 genera respectively, but the number of generic names referable to them approaches 100.

Within this group of plants, there exist three more or less readily recognisable aggregations (plus one very aberrant genus *Schiedea*, including *Alsinidendron*, whose true affinities may well be with the *Paronychioideae*). These aggregations, which do not necessarily follow natural relationships, are what may be described as the *Stellaria-Cerastium* group (including also *Myosoton*, *Holosteum*, *Moenchia* and possibly *Pseudostellaria*), the *Sagina* group (including also *Colobanthus*) and the *Arenaria* group. This last is the largest, both in number of species and in generic diversity. In addition to the generic complex making up *Arenaria* in the very broadest sense, there are five related genera (four of them monotypic) whose distinctiveness has rarely, if ever, been questioned. These are *Thylacospermum*, *Thurya*, *Gooringia*, *Reicheella* and *Buffonia*, the last a very natural Mediterranean genus of 10 species with a characteristic habit. Of the monotypic genera, *Thurya*, confined to the Cilician Taurus in Turkey is very distinct, but the other three could well be no more than extreme derivatives from different groups of *Arenaria*. This is certainly so in the case of the Tibetan genus *Gooringia*, whose one species (*G. littledalei*) is no more than a much reduced representative of *Arenaria* Subgenus *Odontostemma*, with which it has been included in this account. *Thylacospermum*, a densely pulvinate plant of the mountains of Central Asia (including the Himalayas) seems related to *A. densissima* in Subgenus *Dolophragma*, while *Reicheella* from the mountains of Chile would seem either to be related to the South American Subgenus *Dicranilla* or else to be outside this affinity altogether, and related to genera such as *Pycnophyllopsis* or *Plettkea*, with indehiscent fruit.

The following artificial key to the free-styled, capsular members of the *Alsinoideae* defines the *Arenaria* complex of genera.

- 1a. Staminal glands \pm petaloid, opposite the sepals; petals absent; inflorescence usually very lax, thyrsoid or paniculate (Hawaiian Islands) *Schiedea*
- 1b. Staminal glands variously developed, not petaloid; petals alternating with sepals, rarely absent; inflorescence various, often a \pm regular dichasium 2
- 2a. Petals bipartite or deeply bifid, rarely absent; plants usually diffuse with relatively broad leaves; seeds exstrophiolate; capsule opening by twice as many teeth as styles; rootstock without tubers (except some spp. of *Cerastium* with 5 carpels)

Cerastium, *Myosoton* and *Stellaria*

- 2b. Petals entire, emarginate or fimbriate, occasionally absent, or very rarely \pm deeply bifid, if absent leaves subulate or setaceous or plant densely pulvinate or seed strophiolate, if bifid capsule opening by as many valves as styles (2) or rootstock bearing small tubers (and carpels 3), or leaves spiny, setaceous 3
- 3a. Inflorescence an umbel-like cyme with the long pedicels becoming reflexed; seeds dorsally compressed (scutiform with median hilum); capsule cylindrical (C. Europe, Mediterranean and W. Asia)
Holosteum
- 3b. Inflorescence various, never a lax umbel, pedicels usually erect or spreading; seeds spherical or laterally compressed (usually reniform); capsule various, rarely cylindrical 4
- 4a. Carpels 4-5 *Colobanthus*, *Moenchia* and *Sagina*
- 4b. Carpels 2-3 (in a few abnormal flowers 4 or 5) 5
- 5a. Flowers dimorphic; chasmogamous fls. in the axils of the upper leaves, with 5 large, entire or rarely bifid petals and an ovary of 3 carpels; cleistogamous fls. at the base of the stem with petals small or absent; rootstock bearing small tubers; leaves relatively large; plants with habit of *Stellaria* (Alps; C. & E. Asia) *Pseudostellaria*
- 5b. Flowers all chasmogamous or very rarely some in the lower part cleistogamous and then chasmogamous fls. usually with 2 carpels and often fimbriate petals; rootstock without tubers 6
- 6a. Sepals united at the base into a short tube 7
- 6b. Sepals free to the base 8
- 7a. Dense low-growing cushion plants; flowers small (c. 2-3 mm.) with a rather membranous calyx enclosed by the upper leaves; capsule opening by twice as many valves as styles (2-3) (C. and S. Asian mountains) *Thylacospermum*
- 7b. Erect tufted rather spiny plants; flowers rather large (c. 10 mm.) in terminal clusters with the calyx hardened at the base; capsule opening by as many valves as styles (3) (S. Turkey) *Thurya*
- 8a. Sepals and petals 4; stamens (4-)8; carpels 2; plants densely pulvinate with tetrastichous leaves or strictly erect with appressed subulate leaves; seed not strophiolate 9
- 8b. Sepals and petals 5, rarely 4 and then carpels 3 or if carpels 2, capsule opening by 4 valves and either diffuse plants with spreading leaves and strophiolate seeds or small moss-like plants with stamens reduced to 2 "*Arenaria sensu latissimo*"
- 9a. Plants low-growing, densely pulvinate, with ovate tetrastichous leaves with a narrow membranous margin; flowers solitary (capsule unknown) (Chile) *Reicheella*
- 9b. Plants strictly erect with appressed subulate leaves; flowers in a spike or panicle; capsule opening by 2 valves (Mediterranean) *Buffonia*

The aggregation of genera which have at various times been included within *Arenaria* (notably by Bentham in Bentham & Hooker, 1862) has therefore the following diagnosis:

Sepals 5 (rarely 4), free to the base; petals 5 (rarely 4 or 0), entire, emarginate, crenate or fimbriate (very rarely bifid, cf. *Lepyrodiclis*) stamens 10 (or sometimes 5 + 5 staminodes, or rarely reduced to few e.g. 2 or 3); carpels sometimes 2 usually 3; seeds globose or laterally compressed (usually reniform).

There is thus no single character by which genera such as *Buffonia*, *Reicheella* or *Pseudostellaria* can be distinguished from the *Arenaria* aggregate (unless it be the presence of small tubers in the last named). In "*Arenaria sensu latissimo*" however, tetramerous flowers with two carpels are only known to occur in species of *Moehringia* with its distinctive strophiolate seeds and characteristic habit, and in one (or possibly a few) very reduced species of *Arenaria* Subgenus *Odontostemma*—*A. littledalei* (= *Gooringia littledalei*). The discrimination of *Buffonia* with its bicarpellary tetramerous flowers, undivided capsule valves, and very distinct facies, thus presents no difficulty. Doubts as to the generic position of *Reicheella* have already been expressed and in the absence of adequate material from South America its status must remain in doubt; indeed no specimens of *Reicheella* have been seen though it is figured (poorly) in Philippi, 1891 (t.l. f. 7. as *Lyallia andicola*). *Pseudostellaria* (= *Krascheninnikovia*) appears to be a natural, if ill-defined, "buffer" group between *Arenaria* on the one hand and *Stellaria* on the other (cf. Ohwi, 1937, Schaeflein, 1957 and Takeda, 1913).

Generic delimitation in the *Arenaria* group has always been a matter of dispute. For the last 100 years this has involved two opposing viewpoints; the one maintained to-day chiefly by American botanists regards "The unity of the genus *Arenaria*" (Fernald, 1919) as almost axiomatic; the other, generally held by European workers, divides the group into three main genera *Minuartia*, *Arenaria* and *Moehringia* (and a varying number of smaller ones) distinguished technically by the number of capsule teeth or valves and the presence or absence of a strophiole on the seed. Although there is probably some basis for these divergent viewpoints if weight is given to either New or Old World representation alone, it should be noted that this has not always been the case, for both Asa Gray and Small kept the group divided while Bentham and Hooker favoured a single genus. Both the history of the taxonomic treatment of each of these three main divisions and the nature of the variation within each group differ greatly. As a result the present work has taken a different form for each group.

In *Minuartia*, in which the capsule opens by as many valves as there are styles, there are about nine or ten clearly defined natural subdivisions which have been recognised since the time of Fenzl (1840). The genus was very competently monographed by Mattfeld (1922), who proposed a satisfactory classification of these sections. As a result the present contribution will be confined to slight emendations and to corrections in nomenclature.

In *Arenaria* the capsule opens by twice as many teeth or valves as there are styles (or with an equal number of bifid teeth). The infra-generic classification of *Arenaria* is very confused, partly because only a few mostly very large natural groupings stand out and partly because Williams

(1898) employs a rather artificial single-character arrangement which not infrequently overrides recognised affinities. To bring the same degree of clarity to *Arenaria* as exists in *Minuartia* it is necessary to provide a reclassification which refers for its basis back to the major groupings recognised by Fenzl in 1833 and 1840.

By far the smallest of the three main subdivisions of the *Arenaria* group is *Moehringia*, with about twenty species, mostly in Europe. It is distinguished from *Arenaria* s.s. by the presence of a white or brown appendage (strophiole) on the seed near the hilum. The arrangement proposed by Nyman (1854-55; 1878) and followed by Graebner (1915-16) in their accounts of the European species is, on the whole, a satisfactory one.

The smaller genera recognised by many European and other authors include *Brachystemma*, *Moehringella*, *Gouffea*, *Wilhelmsia* (= *Merckia*), *Lepyrodiclis*, *Greniera*, *Hymenella*, *Honkenya*, *Cherleria*, *Rhodalsine* and *Queria*; of these the six last are included by Mattfeld in his monograph of *Minuartia*, while a revision of the three species of *Lepyrodiclis* was recently published by Wagenitz (1957).

HISTORY OF THE CLASSIFICATION OF THE GROUP

In the first edition of "Genera Plantarum" (1737), Linnaeus included only one genus referable to the group, namely *Arenaria* itself, but by 1753, he recognised five genera: *Minuartia* and *Queria*, closely related xerophytic genera with a reduced number of stamens; *Moehringia* with tetramerous flowers; *Cherleria* a monotypic apetalous genus; and *Arenaria* itself with 12 species embracing plants with the capsule splitting by both 3 and 6 valves or teeth.

In passing it may be noted that in 1753 the genus *Alsine* contained two species (now referable to *Stellaria* and *Spergularia* respectively) but in the second edition of "Species Plantarum" (1762) Linnaeus transferred one of the species originally published in *Arenaria* (*Ar. mucronata*) to *Alsine* and thereby initiated one hundred and fifty years of confusion in the application of this name. The exact identity of *Als. mucronata* (L.) L. has not been established but it refers to a species of *Minuartia* (Sect. *Sabulina* or Sect. *Minuartia*—possibly *M. mutabilis*=*M. rostrata*). Stokes (in Withering, 1787) and Villars (1789), both realised the heterogeneity of *Alsine* and the latter transferred the type species *Als. media* to *Stellaria*, *Als. segetalis* to *Spergula* and *Als. mucronata* back to *Arenaria*. Gaertner (1791), however, emphasising the character of capsule dehiscence, took up the name *Alsine* exemplifying it by *Als. mucronata* and the name came to be used for those *Arenarias* with a 3-valved capsule (now correctly known as *Minuartia*). The history of *Alsine* and its displacement with the coming of the type concept has been discussed at length by many writers—e.g. Hiern (1899), Briquet (1910), Moss (1914), Fernald (1919 a and b) and particularly Sprague (1920). Not all these authors have been in agreement on details but the correct application of each name can be seen from the following summary of type species and of the first uniting of genera:

Genus	Type species
<i>Alsine</i> L. (1753)	<i>Als. media</i> L. (= <i>Stellaria media</i> (L.) Vill.)
<i>Arenaria</i> L. (")	<i>Ar. serpyllifolia</i> L.
<i>Cherleria</i> L. (")	<i>Ch. sedoides</i> L. (= <i>Minuartia sedoides</i> (L.) Hiern)
<i>Minuartia</i> L. (")	<i>Min. dichotoma</i> L.
<i>Moehringia</i> L. (")	<i>Moehr. muscosa</i> L.
<i>Queria</i> L. (")	<i>Q. hispanica</i> L. (= <i>Minuartia hamata</i> (Hausskn.) Mattf.)
<i>Stellaria</i> L. (")	<i>St. holostea</i> L.

Genera	first united by	name chosen
<i>Alsine</i> , <i>Arenaria</i> , <i>Moehringia</i> , <i>Sagina</i> , <i>Spergula</i> and <i>Stellaria</i> (together)	Scopoli (1772)	<i>Stellaria</i>
<i>Cherleria</i> and <i>Arenaria</i>	Bentham (1862)	<i>Arenaria</i>
<i>Minuartia</i> and <i>Arenaria</i>	Bentham (1862)	<i>Arenaria</i>
<i>Moehringia</i> and <i>Arenaria</i>	Bentham (1862)	<i>Arenaria</i>
<i>Cherleria</i> and <i>Minuartia</i>	Hiern (1899)	<i>Minuartia</i>
<i>Queria</i> and <i>Minuartia</i>	Mattfeld (1921)	<i>Minuartia</i>

It is clear, therefore, that the name *Alsine* falls into disuse (so long as *Stellaria media* is regarded as congeneric with *S. holostea*), and moreover that when the genera with 3-valved capsules are united (*Cherleria*, *Minuartia* and *Queria*) the correct name for the resultant genus is *Minuartia* and not *Cherleria* as used by Sampaio (1913) or any new name such as *Alsinopsis* proposed by Small (1903).

As has been noted above, Gaertner (1791) was the first to realise the importance of capsule dehiscence in the classification of the group; the validity of the separation into two groups, one with as many valves as styles and one with twice as many valves or teeth, has been a major source of controversy in the taxonomy of the *Alsinoideae* ever since.

The first monographic treatment of the group is in a little known paper by Desvaux (1816) but it was Fenzl who made the most notable contributions to the taxonomy of the *Alsinoideae*. The monograph which he planned was never completed and his chief writings consist of a discussion (1833) of the phytogeography and natural relationships of the sub-family (in which his arrangement of species appears in the distributional tables), and accounts of the group in Endlicher's "Genera Plantarum" (1840) and Ledebour's "Flora Rossica" (1842).

Fenzl (1840) recognised eleven genera within *Arenaria* sensu latissimo—five in the tribe *Sabulineae* in which the capsule split by as many valves as styles, four in the *Stellarineae* with twice as many teeth or valves as styles and two, *Merckia* and *Dolophragma*, in a separate tribe *Merckieae* in which the capsule was reputed to show partial septation. Although some of Fenzl's observations and judgements are certainly wrong, notably the partial septation in *Dolophragma*, each of his genera and infra-generic units are generally accepted to-day as natural groups (with the possible exception of *Queria* and *Dolophragma* closely merged with other species of *Minuartia* and *Arenaria* respectively).

About the same period J. Gay was engaged in extensive studies on the *Alsinoideae* but the only notable publication which resulted was his monograph of the genus *Holosteum* (1845) in footnotes to which there is discussion of members of the *Arenaria* group (*Rhodalsine* and *Greniera*). His manuscripts in the library at Kew show that he was planning an account of all the genera in the Sub-family and was well on the way to completing enumerations of the species of "*Alsine*" (= *Minuartia*) and *Buffonia*. A fragmentary note by Grenier (1841) seems, likewise, to represent the only published part of planned monographic work.

Nyman (1854-55) in his first enumeration of European plants, followed Fenzl in generic delimitation but proposed a classification of *Moehringia* based on leaf shape, which was later adopted and validated by Graebner (1915-16).

Where Fenzl had recognised eleven genera, Bentham (in Bentham and Hooker, "Genera Plantarum", 1862) maintained only three, *Arenaria*, *Brachystemma*, and the monospermic *Queria*. The genera of other authors were mostly accommodated as the eleven subgenera or sections into which he divided *Arenaria*.

Apart from Seringe's (1824) rather ill-arranged conspectus of species and accounts in regional floras (e.g. Reichenbach 1832, 1842), Fenzl in Ledebour (1842), Grenier and Godron (1847), Boissier (1867), Rohrbach (1872) and Edgeworth and Hooker (1874), there was no revision of any part of the group at species level until Williams published his detailed classification of *Arenaria* in 1895, and followed it in 1898 with a full enumeration of species with references, synonymy and often descriptions. This account is marred by his tendency to base his classification on single characters, and particularly his use of characters which are not always homologous throughout the genus (e.g. "smooth" seeds). The basis of his classification is that of Fenzl, and while some of his modifications reveal new neutral groupings (e.g. *Leiosperma*), others divide up homogeneous groups among unrelated species (e.g. his use of staminal gland structure to spread the species of *Eremogone* into three different subgenera).

1899 to 1921 was the period of the changeover from the misuse of *Alsine* to the adoption of *Minuartia* for the "unspecialised" species with three-valved capsules. In 1921 and 1922 Mattfeld published his monograph of *Minuartia* with a detailed discussion of taxonomic criteria and generic limits. His conclusions were that there is a fundamental distinction between the loculicidal capsule of *Minuartia* and its allies and the loculicidal and septicidal structure in *Arenaria*, *Moehringia*, *Stellaria*, *Cerastium*, etc. (cf. Mattfeld 1922a). Like Williams, Mattfeld based his classification on that of Fenzl but was more successful in defining smaller natural groupings.

In the last thirty-five years, there have been three notable contributions to the taxonomy of the group; the first was the enumeration of the Chinese species by Handel-Mazzetti in "Symbolae Sinicae" (1929) which to some extent drew together the numerous species published between 1905 and 1920 by Williams, Diels and W. W. Smith; in 1936, Schischkin's (and others') account of the Caryophyllaceae in the Flora U.R.S.S. was published and in this some new infra-generic groups of *Arenaria* were proposed (but without validating Latin diagnoses); thirdly the North

American members of the group were the subject of studies by Maguire which culminated in the publication in 1951 of a conspectus of the species occurring north of Mexico. Of these authors the first two regarded *Arenaria*, *Minuartia*, *Moehringia* and other groups as distinct genera, while Maguire treats each as a section of *Arenaria*.

Individual sections or species aggregates have been the subject of study by a number of other botanists, notably Turrill (1932), Kharadze (1938), Pawlowski (1939), Font Quer (1948) and Nannfeldt (1954).

CRITERIA OF CLASSIFICATION

Before considering the status of the widely recognised subdivisions of *Arenaria sensu latissimo*, it is desirable to examine some of the characters which have been used in the classification of the group and to assess their validity.

Habit:

Habit is perhaps the most variable feature in the group; very small slender annuals, densely pulvinate alpine, spiny suffrutescent plants, succulent maritime herbs, xerophytes of Mediterranean and steppe climates and lax broad-leaved mesophytes are all to be found. The taxonomic importance rests in the fact that both Fernald (1919) and Maguire (1951) have rejected the splitting of the genus *Arenaria* largely because when this is done, plants of very similar habit are generically separated, while the genera created have usually no distinct facies.

Although predominantly mesophytic, *Stellaria* and *Cerastium* show a range of structure paralleling that found in the *Arenaria* group, while in the subfamily *Silenoideae* habit parallelism is even more marked and many species of *Gypsophila*, *Dianthus*, *Saponaria*, etc. are scarcely distinguishable in the vegetative state from those of *Arenaria* or *Minuartia*. In view of the fact that all these groups are widely distributed over a similar geographical and ecological range this parallelism is not surprising and on the basis of habit alone there is as much justification for uniting *Arenaria* and *Minuartia* as there is for linking *Arenaria* and *Gypsophila*.

Inflorescence:

The dichasial cyme is the characteristic inflorescence type in the *Arenaria* group as in the family as a whole, but departures from this form, notably the reduction to the solitary condition (often in dwarf alpine) and the aggregation of flowers into heads, have frequently been the basis of taxonomic groupings. With one exception these represent evolutionary trends which have occurred independently in unrelated groups; the diversity of floral structure and the presence of intermediate conditions make this quite certain. (cf. treatment of the glomerate inflorescence species of *Arenaria* Subgenus *Eremogone*, i.e. Williams' "*Glomeriflorae*"). The exception is a Himalayan group of species of *Arenaria* (Subgenus *Solitaria*) where large solitary terminal flowers are the rule and which shows no evidence of inflorescence reduction; indeed no closely related species with a cymose inflorescence are known.

Axillary flowers occur in a number of mesophytic species; Mattfeld (1922a) claims that in *Honkenya* these represent the successive flowers of a modified monochasium which have been pushed into a lateral position.

This interpretation is probably also true of some groups of *Arenaria*, and although this feature characterises a few apparently natural groupings (*Odontostemma*, *Leiosperma*) it again is one which has probably developed independently in different lines.

The nature of the bracts, whether leaf-like or setaceous, seems also to be of importance in delimiting some groups.

Flowers:

Reduction in the number of perianth parts and in the number of stamens and carpels is not infrequent in the *Arenaria* group, as in other members of the *Alsinoideae*. In most cases connecting links with plants having a pentamerous perianth, ten stamens and three carpels, are known. Where intermediates are absent other criteria have been taken into consideration in assessing each case on its merits. Thus the tetramerous bicarpellary *Buffonia* with about a dozen species, all with a characteristic facies has been maintained as a distinct genus, while the monotypic *Gouffeia* only differing from *Arenaria* Subgenus *Arenaria* in having two carpels has been given subgeneric rank (*Arenaria* Subgenus *Odontostemma* has also only two carpels).

Sepals:

The sectional classification of *Minuartia* rests primarily on sepal structure, in particular on the shape of the apex and the number and nature of the nerves which are usually very prominent. Most of the major groups have an almost uniform nerve-structure. This is not true of *Arenaria* or *Moehringia* where the nerves are usually much less distinct and can be very different in structure in apparently closely related species. The general form of the sepals seems to be more constant, as for example the hardened sepals of Subgenus *Eremogone* and the truncate-saccate ones in Subgenus *Odontostemma*.

Petals:

Petal reduction is not uncommon throughout the group, particularly in self-pollinating annual species and in some high mountain plants. As such, it occurs independently in a number of groups and the presence or absence of petals is rarely of significance above the species level. The relationships of apetalous species such as *Minuartia hamata* (= *Queria hispanica*) and *Minuartia* (*Cherleria*) *sedoides* with corolliferous members of the genus *Minuartia* are very close.

Staminal Glands:

Williams (1895, 1898) based his classification of *Arenaria* primarily on staminal gland structure and in so doing destroyed a number of natural groupings without creating any new circles of affinity (at least on the basis of gland form). He recognised three conditions—no glands, five glands at the base of the outer stamens and ten glands arranged between the stamens. These became the unit character criteria of his three large subgenera, "*Euarenaria*", *Pentadenaria* and *Eremogoneastrum*. In *Minuartia*, exactly the same range of staminal gland structure exists, and a comparison with that genus might have warned Williams of the danger of resting so much of his classification on this one character alone.

Contrary to Williams' claims, the glands (or equivalent structures) are always present and are always associated with the outer whorl of stamens.

Williams' "absence of glands" means very reduced structures which may or may not be glandular, but which show a continual gradation, at least on herbarium material, to the prominent "five-gland" condition. These glands generally lie on the exterior side of the stamens and appear from that angle as rectangular flaps or swellings in front of the base of the filament. Viewed from the interior of the flower they appear when well-developed as two swellings, one on either side of the filament base. In many species there is a median nectar groove which sometimes tends to make the gland appear emarginate or in some species almost crescent-shaped. In *Minuartia* Section *Minuartia* this development can be traced to a bifurcate condition in which the glands appear superficially to be ten in number. In some species the nectar furrow remains between the 'horns' of the gland, but in most the secretion is to be found in a cup-shaped pit at the tip of each of the finger-like divisions of the gland (for illustrations cf. Mattfeld, 1938). As one would expect, if these glands have an attractive function, this is most often an "all or nothing" condition and species which in other characters are almost identical will have on the one hand single glands with a medium nectar furrow and on the other bifurcate structures with apical nectar pits. This is seen most clearly in the distinctive localised *Minuartia bosniaca* and the polymorphic *M. setacea* which can scarcely be satisfactorily separated except by the fact that the former possesses prominent bifurcate glands. A similar situation holds with *M. decipiens* (glands single) and *M. intermedia* (glands bifurcate) but it is complicated by the existence of an intermediate race (*M. decipiens* ssp. *damascena*) which has some of the characters of *M. intermedia* but the glands and pubescence of *M. decipiens*.

In *Arenaria* itself very similar species such as *A. lychnidea* and *A. capillaris* (treated as conspecific by Regel, 1862) have minute and prominent glands respectively, and Williams consequently places the one in subgenus "*Euarenaria*" and the other in subgenus *Pentadenaria*. In the same way *A. cucubaloides* and *A. gypsophiloides*, which are satisfactorily distinguished only by flower size and the length of the leaf sheaths, are widely separated from one another in his classification.

The most complex staminal gland structure occurs in *Minuartia douglasii* (Section *Greniera*) in which there is a prominent broad flap behind the nectar furrow, and the filament clearly arises in a lateral position in front of the furrow (cf. Mattfeld 1922, 1922 a.). The related species, *M. howellii*, has well-developed simple glands and provides a connecting link with Section *Sabulina* and other annual groups of *Minuartia*.

Gynoecium:

Mattfeld (1922a) has discussed at length the importance of carpel number and arrangement in the *Alsinoideae* as a whole; he concludes that in the isomeric condition (i.e. carpels equal in number to the perianth parts), arrangement is very important, but that reduction in number occurs both in plants with antisepalous carpels and those with antipetalous ones. Moreover he found that it was impossible to determine whether a reduced trigynous ovary had originated from the antisepalous or antipetalous condition, except by the implications of close affinity (e.g. in trigynous *Cerastium* spp.). It seems likely that reduction from

five to three carpels has occurred in a number of separate lines, just as further reduction to two carpels is seen in widely separated members of the *Arenaria* group. (*Moehringia* Section *Moehringia*, *Arenaria* Subgenera *Odontostemma* and *Arenariastrum*, *Lepyrodiclis*, *Brachystemma* and the distinctive genus *Buffonia*).

Of all gynoecium characters the one whose evaluation has the most far-reaching consequence is, of course, that of capsule dehiscence, the recognition of which we owe to Gaertner (1791). Much has been written on this subject, a lot of it polemic and based on preconceived ideas and inaccurate observations. As Mattfeld has demonstrated and as all the present writers observations confirm, there is no doubt that capsule dehiscence in all the known members of the group takes place in one of two quite different ways—either along the midline of the individual carpel (i.e. opposite the styles: loculicidal), or else both in this position and along the line of carpel fusion (loculicidal and septicidal). (The dehiscence of the fleshy capsule of *Wilhelmsia* (*Merckia*) was not known to Mattfeld, but it appears that when it occurs it is loculicidal—along the line of the partial (false) septa). As Mattfeld has shown, these are not chance lines of fracture but are predetermined at an early stage by the distribution of vascular tissue in the ovary wall. This being so, it is not altogether surprising that no examples are known of affinity running across the difference in capsule dehiscence. The supposed cases cited by Fernald (1919), Maguire (1951), etc. represent superficial habit similarities which appear more important in the impoverished *Arenaria*/*Minuartia* flora of North America than when viewed against a world-wide background. Indeed, in Eurasia a more extensive list of species of the two genera which are very similar in form and habit could be drawn up. In each case the examination of usually reliable characters (e.g. in the flower) shows clearly that their closest affinities are with members of their own genus; their superficial resemblance to species of the other genus is due to the same sort of habit parallelism that we find between species in the *Silenoideae* and *Alsinoideae* (e.g. *Arenaria cretica* and *Gypsophila nana*).

In *Arenaria* there is some variation in the extent to which the capsule opens; this variation seems to be directly correlated with the texture of the capsule at time of dehiscence. Thin membranous capsules usually split to the base by six valves, while more coriaceous ones open by valves or teeth of varying depth and sometimes, but not often, the locular division is deeper than the septal one, so that the capsule opens by "three bifid teeth". In ligneous capsules, which are often flask shaped, the teeth are usually very short. There would appear to be no clear-cut distinction between any of these conditions and they seem to have little taxonomic significance, although in groups such as Subgenus *Eremogone* in which the capsule is usually ligneous, dehiscence is always by short teeth. In *Minuartia* and *Moehringia*, only valvular dehiscence of membranous to coriaceous capsules is known.

In at least one species of *Minuartia*, *M. hamata*, often regarded as forming a monotypic genus *Queria*, the one-seeded 'capsule' is often functionally indehiscent, the partial inflorescence being the unit of dispersal and the seeds often germinating *in situ*. That it is essentially a three-valved structure is obvious because the lines of dehiscence are very clear and the capsule can be dissected open at a touch along these lines.

Seeds:

Mattfeld makes considerable use of seed characters, particularly the structure of the testa, in his classification of *Minuartia*, while Williams noted that many species of his *Arenaria* Subgenus "*Euarenaria*" had smooth shiny seeds (his Section *Leiospermae*). Most important of all, the genus *Moehringia* is fundamentally distinguished from *Arenaria* only by its strophiolate seeds.

All the species of the group possess laterally flattened seeds, which are often reniform, with the exception of *Brachystemma* in which the seed is subglobular (slightly laterally compressed near the hilum), the very broad cotyledons being incumbent and laterally folded near the apex. The normal reniform seeds are very regular in shape in most mesophytic species, but in xerophytic plants often appear to suffer distortion under pressure in the developing capsule; the seeds of *Arenaria* Subgenus *Eremogone* and *Minuartia* Subsection *Xeralsine* are notably irregular. Frequently the seed is longitudinally compressed so that the long diameter runs from the hilum to the dorsal ridge; such seeds are often more or less pyriform and this is the normal condition in *Honkenya* and *Arenaria* Subgenus *Eremogone*. In at least two groups the seeds are strongly compressed and to a greater or lesser extent winged by an extension of the testa in which no endosperm is laid down; in *Minuartia* Section *Greniera* the main part of the seed is reniform, but in *Arenaria* Section *Compressae* the seed is broadly ovate in surface view with the long axis from the hilum to the dorsal ridge. In some species normally placed in *Arenaria* Subgenus *Odontostemma* a so-called "winged" seed is formed by the inflation of the testa; here, however, the seeds are not compressed. On account of this feature and a strophiole-like structure (see below) Neumayer, in 1924, raised to generic rank Franchet's Section *Moehringella* to contain two such species. From the few seeds available of members of Subgenus *Odontostemma*, it would appear that this is the usual condition in the subgenus; it is not recorded elsewhere in the group.

The seeds vary in colour but in *Arenaria* and *Moehringia* appear to be either reddish or more often an intense black; a notable exception is *A. compressa* (Section *Compressae*) in which the mature seed is a buff colour. In *Minuartia*, on the other hand, even the most fully ripened seeds are no more than a very dark brown while in some species mature seeds may be straw-coloured. Seeds which remain a pale colour on maturity (i.e. red or straw) are also those which lack prominent sculpturing, having a thin seed coat.

The terminology used to describe the form of the testa of species of the group is very confused, partly because the description tends to vary with the magnification at which the seeds are viewed and partly because the same term has been used for two totally different kinds of seed coat, sometimes even by the same author. In most groups the seeds are of the typical Caryophyllaceous sort in having a testa bearing distinct cellular markings. These "cells" are often convex in surface view and particularly on the dorsal ridge frequently develop into the tubercles of tuberculate seeds (e.g. in *Arenaria* Section *Arenaria* and *Minuartia* Section *Sabulina*). In other species the seed surface is quite smooth but with these distinct (at $\times 10$) cellular markings; such seeds are described throughout this account as *obscurely reticulate* (e.g. *Arenaria balansae*). In the past such

seeds have generally been termed *smooth* but they are quite different from the sculptureless (at $\times 70$) shiny seeds (as in *Arenaria* Subgenus *Leiosperma* and most species of *Moehringia*) to which this term is now confined. This confusion led Williams to place a number of Eurasian species of other groups (e.g. *A. halacsyi* and *A. balansae*) in his otherwise natural South American *Leiosperma*, but as there is no essential difference between the tuberculate and obscurely reticulate condition, it is not surprising that they are sometimes found in closely related species or groups of species.

Tuberculate or obscurely reticulate seeds very frequently bear further markings on the "cells" or tubercles. The most common type is the central spot marking which on the cells of the dorsal ridge, in particular, is often produced into a distinct papilla. Such seeds are here termed *papillose*, even if the papillae are only visible at high magnification (e.g. $\times 35$). Often, however, the dorsal papillae (and sometimes the others also) are very large and prominent so that the seeds or merely the dorsal ridge can be described as *echinate*. Seeds with a *fimbriate* crest have in fact extremely long dorsal papillae which are often laterally fused to one another; the brown strophiole of *Moehringia* Section *Pseudomoehringia* may be derived in a similar way from the cells near the hilum. (The typical *Moehringia* strophiole is a totally different whitish amorphous body).

At least one variation on the truly smooth testa structure is known; this is the presence of minute papillae all over the otherwise sculptureless seeds and is a feature of *Moehringia pentandra*. The structure is similar in *Arenaria hispanica* but the papillae are more dense and the seeds lack the lustre of those of *Moehringia* and *Arenaria* Subgenus *Leiosperma*.

Seeds which bear convex cells but are scarcely tuberculate are generally described in the literature as *rugulose*, but in this account the term *obscurely tuberculate* is generally preferred. Where, however, the cell pattern is not clear, as in immature seeds, or where the "cells" are very long and narrow and the wrinkles between them prominent, or in groups such as *Eremogone* or *Honkenya* with very small cells, the term *rugulose* has been retained.

Finally there are those seeds which are not smooth in the strict sense of the word but which at $\times 70$ magnification have no very prominent cell markings; such seeds have simply been termed *rough* and seem to occur in *Arenaria* Subgenera *Odontostemma* and *Eremogoneastrum* (although mature seed of the latter has not been seen).

The only other external seed character which has been used in the classification of the group is the presence or absence of a strophiole, a waxy or oily appendage near the hilum. This structure is only well-developed in *Moehringia*, of which it is the diagnostic character, but in at least some species of *Arenaria* Subgenus *Odontostemma* there is a small protrusion of the testa near the hilum, which is opaque and strophiole-like; contrary to Maguire's (1951) assertion, no trace of a hilum appendage could be detected in *Wilhelmsia* (\equiv *Merckia*).

It has already been noted that the strophiole of *Moehringia* Section *Pseudomoehringia* differs from that of other species of the genus in being a brown colour and composed of long "papillae" densely packed together. In the rest of the genus the strophiole is a white amorphous body and there must be some doubt as to whether the two structures are homologous. Both are rather oily and serve to attract ants which act as dispersal agents.

Cotyledons:

In most species the cotyledons are incumbent (i.e. they are 'back-on' to the radicle and therefore 'back-on' to the endosperm on one side and the dorsal ridge on the other); as a result the ridge is not normally grooved. In certain groups, however—*Minuartia* Subgenera *Rhodalsine* and *Spergella* and *Arenaria* Subgenera *Eremogone* (excluding Section *Pungentes*) and possibly *Eremogoneastrum* and *Dolophragma*, the cotyledons are in the accumbent position and 'edge-on' to the radicle, endosperm and dorsal ridge; in this case the dorsal ridge is frequently deeply grooved. *Arenaria* Subgenus *Odontostemma* has incumbent cotyledons but these are frequently laterally folded near the top, the upper portion being either doubled under the main part or twisted into an accumbent position. This folding over of the cotyledons also occurs in *Brachystemma* which in seed characters shows a possible origin in an *Odontostemma* stock. A cotyledon, form, which, so far as is known, is unique in the group, is found in *Arenaria compressa*, the only species of Section *Compressae*. The broad cotyledons in the strongly compressed seed have retained their incumbent arrangement but have become longitudinally folded away from the radicle (i.e. the reverse of orthoplocous).

Cytology:

Relatively little cytological work has been done on the group as a whole, although chromosome counts have been made of most of the North European species. Because the counts are so unrepresentative, no very definite taxonomic conclusions can be based on them, but from the existing data certain trends and constant features seem discernible. The chromosome number of thirty-one species of *Arenaria* (out of about 250) has been reported; all but six of these are members of Subgenus *Arenaria*. The earlier counts suggested that there was a constant base number of $x=10$ in the genus but recently Favarger (1962) has shown that the base number 11 is very common and that the haploid numbers, 9, 12, 13, 14, 15 and 23 also occur. While discrepancies exist there is a suggestion that the following taxonomic groups may have a characteristic chromosome base number:

Subgenus <i>Porphyrantha</i>	$x=23$
Subgenus <i>Arenaria</i>	
Sections <i>Rariflorae</i> and <i>Arenaria</i>	$x=10$
Sections <i>Rotundifoliae</i> and <i>Orietales</i>	$x=11$
Subgenus <i>Arenariastrum</i>	$x=10$
Subgenus <i>Eremogone</i>	$x=11$

In addition, Beaman, de Jong and Stoutamire (1962) have reported counts on one species of Subgenus *Leiosperma* (*A. parvifolia*— $2n=44$) and one of Subgenus *Dicranilla* (*A. bryoides*— $2n=ca. 54$).

Seven species of *Moehringia* representing the Sections *Latifoliae*, *Diversifoliae* and *Moehringia*, have been examined cytologically and a constant base number of 12 found. Böcher and Larsen (1958) note that the chromosomes of *Moehringia trinervia* are much larger (and longer) than those of *Arenaria serpyllifolia* or *A. leptoclados* and suggest that this is an added justification for the maintenance of the two genera. Important though this may be, it should be noted that on morphological grounds *Moehringia* is in any event far removed from these species of *Arenaria*,

and what would be much more revealing would be a comparison with, for example, *A. lanuginosa* (Subgenus *Leiosperma*).

The thirty-two investigated species of *Minuartia* (one in Subgenus *Rhodalsine* and the remainder in nine sections of Subgenus *Minuartia*) show a very heterogeneous assemblage of recorded numbers ($x=9, 10, 12, 13, 14, 15, 16, 18, 23$) including considerable variation in counts of the same species. (The small size of the chromosomes and difficulties of identification of the species, have led to considerable inaccuracy in early work). The existing data suggest that Subgenus *Rhodalsine* may have a base number of 9, and that the following base numbers are characteristic of sections of Subgenus *Minuartia* accepted on morphological grounds:

<i>Spectabiles</i> (including		<i>Tryphane</i>	$x=12, 13$
<i>Cherleria</i>)	$x=13$	<i>Alsinnanthe</i>	$x=13$
<i>Plurinerviae</i>	$x=15$	<i>Uninerviae</i>	$x=10$
<i>Lanceolatae</i>	$x=18$	<i>Minuartia</i>	$x=14, 15$
<i>Acutiflorae</i>	$x=13$	<i>Sabulina</i>	$x=11, 12, 23$

The most confused species in respect of published counts is *Honkenya peploides* where the diploid numbers 48, 64 and 66 have been recorded by Rohweder (1939) and Flovik (1940), but Malling (1957), who counted $2n=68$ in all his material, has given good evidence for believing that all the previous counts were erroneous; Blackburn and Morton (1957) have since reported the records of $2n=48$ and $2n="c. 64"$, once again, while Sokolovskaya and Strelkova (1960) record $2n=68-70$.

EVALUATION OF GENERA AND GENERIC LIMITS

Although the *Arenaria* group contains about fifty validly published generic names, only fifteen of these have been extensively recognised or employed by recent authors, and the present discussion will be confined to them.

These genera fall very clearly into two groups—those in which the capsule opens by twice as many teeth or valves as there are styles and those with an equal number of valves. The former comprises *Moehringia*, *Brachystemma*, *Gooringa*, *Gouffeia*, *Moehringella* and *Arenaria* itself, while the remaining nine genera fall into the latter division (i.e. *Minuartia*, *Cherleria*, *Greniera*, *Honkenya*, *Hymenella* (*Triplateia*), *Lepyrodictis*, *Queria*, *Rhodalsine* and *Wilhelmsia* (*Merckia*). The constancy of the capsule dehiscence character has already been stressed (cf. pp. 89-90) and the important fact mentioned that there are no similarities between species in the two groups that are not more easily explained by habit convergence, than by true affinity. This would suggest that these two groups of plants represent separate lines of evolutionary development just as the sub-families *Silenoideae* and *Alsinoideae* may be presumed to do from an even earlier level. Indeed it is not unlikely that *Arenaria* and *Moehringia* are more closely related to *Stellaria* and *Cerastium*, also with divided capsule valves, than they are to *Minuartia*, *Buffonia*, etc.

This is the theoretical basis for the decision to accept this major subdivision of the *Arenaria* group and in particular to maintain *Arenaria* and

Minuartia as separate genera. The practical basis rests in the fact that, although the capsule dehiscence character is the only one which is known to be universally constant throughout the group, once the sectional characters of each genus are known, there is never any difficulty in assigning a non-fruitlet specimen to its correct genus.

To maintain *Arenaria* and *Minuartia* is to make no departure from the general practice of contemporary botanists (except those in North America) and is in accord with the separation of *Lychnis* from *Silene* in the *Silenoideae* (cf. Chowdhuri, 1957), where the same character of capsule dehiscence provides the most natural arrangement of the genera.

Having decided to maintain the two major genera, there remains the not so far-fetched, but much more difficult task of determining the status of each of the thirteen frequently recognised smaller groups, and also of some of the more outstanding groups of *Arenaria* and *Minuartia* themselves. The genera will now be considered in turn, dealing first with those which resemble *Arenaria* in having divided capsule valves.

Moehringia:

This is the largest and most important of all these genera and is the only one which has enjoyed the same widespread recognition as *Minuartia*; indeed many of its species have no published name in *Arenaria*. The genus was regarded as a very homogeneous group until it was recognised that in *M. intricata* and *M. tejedensis* etc. (Section *Pseudomoehringia*) it included species which, although possessing a strophiole, were very atypical in their seed characters and approached *Arenaria* Subgenus *Arenaria*. It is quite possible that these species are in fact true *Arenarias* and that their strophiole is a totally different structure from that found in *Moehringia* proper. The latter in its smooth shiny lenticular seeds, its sometimes solitary axillary flowers and its general habit, most closely resembles the predominantly South American *Arenaria* Subgenus *Leiosperma*. The two groups come geographically closest in North America where *Moehringia lateriflora* and *M. macrophylla* are distinguished from *A. lanuginosa* (with a taproot) by their rhizomatous habit. This resemblance may, of course, merely represent yet another example of habit parallelism.

It seems likely that even excluding Section *Pseudomoehringia*, *Moehringia* is not more distinct from *Arenaria* Subgenus *Leiosperma* than are the other subgenera (e.g. *Eremogone* and *Arenaria*) from one another. A representative sample of European species of *Moehringia* (excluding Section *Pseudomoehringia*) has been investigated cytologically and a constant base number of 12 reported; in *Arenaria* Subgenus *Arenaria*, on the other hand, the most frequent base numbers are 10 and 11. Strong evidence on the generic status of *Moehringia* would almost certainly be provided by cytological data for species of *Arenaria* Subgenus *Leiosperma* and for the North American species of *Moehringia* and those in Subgenus *Pseudomoehringia*. Until this and other evidence is available, it seems undesirable to make any major changes in generic circumscription, particularly where this involves new combinations. The genus *Moehringia* is therefore maintained in its currently accepted form, but noting not only that it may prove heterogeneous (Section *Pseudomoehringia* being

aberrant) but also that typical *Moehringia* may have no stronger claims to generic rank than *Eremogone* or *Odontostemma*.

Brachystemma:

This genus of one or possibly two species has the distinction of being one of the two which Benthham (1862) maintained as distinct from *Arenaria*. Indeed apart from its inclusion by Williams (1898) in his Subgenus *Arenariastrum*, it has enjoyed universal recognition. Williams, moreover, had obviously no real understanding of this group or of the two "Sections" which he included with it—*Gouffeia* and *Lepyrodiclis*.

The type species *Brachystemma calycinum*, is in a very isolated position taxonomically, and no affinities with other plants can be suggested unless possibly a remote connection in cotyledon structure with *Arenaria* Subgenus *Odontostemma*. (The second, recently described species, *B. ovatifolium* has not been seen and it is not clear from the description that it is correctly placed). In its specialised inflorescence, scarious sepals and reduced gynoeceum it shows highly advanced characters, while it is probably primitive in its *Stellaria*-like habit, though it is a struggling climber. There is no doubt that *Brachystemma* is best regarded as a distinct genus, in the general affinity of *Arenaria*, but having almost certainly followed a separate line of evolution from a very early stage in the development of the *Alsinoideae*.

Goorlingia:

Williams described this monotypic genus in 1897 on the basis of Hemsley's tetramerous, bistaminate, bicarpellary *Arenaria littledalei*; as is noted elsewhere (p. 81), this plant is no more than an extremely reduced representative of *Arenaria* Subgenus *Odontostemma*, very close to *A. reducta* and *A. inconspicua*, and the genus is therefore reduced to synonymy under that subgenus.

Gouffeia:

As noted above, Williams included this monotypic group in his bicarpellary Subgenus *Arenariastrum*; the single species, a native of Southern France, is a slender annual or biennial plant with subulate or setaceous leaves and in most respects resembles *Arenaria* Subgenus *Arenaria*, of which it is probably a bicarpellary derivative. The chromosome base number of 10 is very common in Subgenus *Arenaria*. There is, however, no group of that subgenus to which it can be attached (unless possibly Section *Occidentales*) and in view of the importance of the bicarpellary condition in other parts of the genus (e.g. Subgenus *Odontostemma*) it has been maintained as a Subgenus separate from, but close to *Arenaria* itself. Williams' Section *Gouffeia* has been chosen as the type section of his Subgenus *Arenariastrum* (cf. pp. 118–119) and so this becomes the correct name for the group at Subgeneric rank.

Moehringella:

This genus was proposed by Neumayer (1924) (taking up Franchet's Section of *Arenaria*) on the basis of its seed having an inflated ("winged") testa. The genus has never been adopted since and Handel-Mazzetti (1929) has shown that this feature is to be found in a number of species typical of *Arenaria* Subgenus *Odontostemma*. Although in the present

work it has only been possible to examine seed of a few species of *Odontostemma*, an inflated testa has always been found. There can be no question of *Moehringella* being generically distinct from the species of *Arenaria* Subgenus *Odontostemma*, and at most it may represent a section of this group (cf. pp. 128-129).

Arenaria:

Since the middle of the last century the circumscription of *Arenaria* has been a very wide one and has included such groups as *Eremogone*, *Dolophragma* and *Odontostemma*, which had originally been regarded as separate genera. On the whole, the wider circumscription appears to be the more desirable on the basis of present knowledge, but it should be noted that some of these groups stand in a very isolated position. Subgenus *Eremogoneastrum* may have branched off early from a primitive *Eremogone* stock, but neither of these groups shows any close relationship with the rest of the genus (unless to Subgenus *Solitaria* by way of Subgenus *Dolophragma* whose affinity is uncertain). Likewise although the existence of species such as *A. glanduligera* suggests that *Odontostemma* and *Solitaria* are probably related, no connecting species have been observed between them (taken together) and *Arenaria* and *Arenariastrum*, on the one hand, and *Leiosperma* and *Dicranilla* on the other (cf. fig. 1).

Cherleria:

Turning to the "Minuartia Series" with undivided capsule valves, the first to be considered is the usually apetalous Linnaean genus *Cherleria*. Until the time of Fenzl (1840) it had been treated as a habit genus for densely pulvinate mountain plants, but he noted the close relationship of the type species, *Cherleria sedoides*, with what is now *Minuartia* and, removing the discordant elements, made *Cherleria* a monotypic division of the genus he termed "*Alsine*". This treatment has been generally followed since, notably by Graebner (1918), Mattfeld (1922), Hayek (1924) and Pax & Hoffmann (1934), but recently Clapham in Clapham, Tutin & Warburg (1952) has restored it to generic rank. That this has been done very arbitrarily is strongly suggested by the fact that Clapham records *Cherleria* as comprising about twelve species, whereas the group, whatever its rank, has been unquestionably demonstrated, for more than a 100 years, to be monotypic. (Except under Sampaio's (1913) circumscription, in which it is equated with the whole of *Minuartia*; the latter name, being chosen by Hiern (1899) for the united genus, has priority—cf. p. 85).

As Mattfeld (1922a) notes, *Cherleria* is very close to *Minuartia* Section *Spectabiles* and shares with it the linear obtuse sepals which are not found elsewhere in the genus, and according to Favarger (1959), both have a chromosome base number of 13. In the opinion of the present author there is no justification (other than tradition) for excluding it from Section *Spectabiles* and it has been included as one of its three subsections. As an alpine group it very closely parallels in habit and ecology the predominantly Arctic Subsection *Spectabiles*, which differs chiefly in its larger petals, erect sepals and less prominent glands.

Greniera:

The type species (*G. douglasii*) of this North American annual group is very distinct from all others in the *Minuartia* affinity in its discoid seeds

with a broad wing and in the structure of its prominent staminal glands (cf. p. 89). *Minuartia howellii* which Mattfeld and many American authors relate to *M. douglasii* has well developed simple glands and rather flattened narrowly winged seeds. Whether or not it should be included in *Greniera* is open to question, but it certainly provides a link between *M. douglasii* and the other species of *Minuartia*.

In other characters both species are typical of *Minuartia* and have filiform leaves and the general facies of the genus. Mattfeld (1922) treats *Greniera* as a section of *Minuartia* and this has been followed in the present account.

Honkenya:

Like *Cherleria*, *Honkenya* comprises a single distinctive habit type, but in this case one which is not met elsewhere in the group, although approached in the riparian *Wilhelmsia* (\equiv *Merckia*) with its inflated, partially septate capsule. Mattfeld (1922, 1922a) was of the opinion that as most of the diagnostic characters were probably associated with its maritime habit it should be included within *Minuartia*; in this he was followed by Hayek (1924). Authors such as Williams (1909), Graebner (1918), Pax & Hoffmann (1934) and Gorschkova in Komarov (1936) (as *Ammodenia*), in maintaining it as a distinct genus, have obviously been impressed by the axillary flowers and broad ovate fleshy leaves not met with anywhere in *Minuartia*, though the latter are approached in the very distinctive group *Rhodalsine*. Malling (1957) has also provided what he considers to be cytological evidence in support of its generic status, but although the base number of 17 (assuming Malling is correct, cf. p. 94) has not so far been recorded elsewhere in the group, variation in base number in *Minuartia* is apparently very great.

Perhaps the most important point in relation to its generic evaluation is its complete isolation from the rest of the group in every respect, not merely in habit. Short of the discovery of some new species which would connect it with a known group of *Minuartia*, *Honkenya* will probably always remain one of these small distinctive taxa whose rank is continually in dispute. Its distinctive facies, so unlike that of *Minuartia*, and its complete isolation have been the determining factors in the decision to maintain it as a distinct genus (for the diagnostic characters cf. key p. 101).

Hymenella:

This is yet another distinctive monotypic group in the *Minuartia* affinity (in this case a native of Mexico), which with its quadrangular stems and reflexed sepals and capsule-valves has a rather distinct facies. It has, however, the typical narrow leaves of *Minuartia* and in the absence of any additional evidence it has been decided to follow Mattfeld's (1922) view and include it in *Minuartia*. In view of its distinctiveness and doubt as to its nearest relatives, it has been raised to subgeneric rank along with two other very isolated groups which Mattfeld treated as sections of *Minuartia*.

Lepyrodiclis:

Lepyrodiclis is the only bicarpellary member of the *Minuartia* group, and as it combines with this a very distinctive *Stellaria*-like habit its generic validity has rarely been questioned. The type species was originally

included with *Gouffeia* as the bicarpellary equivalent of the (at that time) tricarpellary *Arenaria s.l.*, but its entire capsule valves were recognised by Fenzl (1840) who established the genus. Williams' (1895, 1898) inclusion of it in *Arenaria* was due to his failure to realise that the valves were undivided. The genus, which consists of three annual species in South and Central Asia, is here maintained, being regarded as a very early offshoot of a primitive *Minuartia* stock, which while retaining the mesophytic habit is highly evolved in the reduction of the gynoeceum, paralleling the very different xerophytic genus *Buffonia*.

Queria:

Originally distinguished from *Minuartia sensu stricto* (= *M. Series Minuartia* and *Campestres*) by its solitary seed, the placing of this Linnaean genus, now regarded as monotypic, has in the past been subject to considerable uncertainty. The small petals and often functionally indehiscent "capsule" have prompted its inclusion in the *Paronychioideae* (e.g. by de Candolle, 1828). Fenzl (1833) united it with "*Alsine*" (= *Minuartia*) but restored it to generic rank in 1840. Bentham (1862) kept the genus distinct from *Arenaria* and placed it between *Schiedea* and *Spergula*. Mattfeld (1922, 1922a) demonstrated its close relationship with *Minuartia* and included it within Series *Minuartia* (*M. dichotoma* and *M. sclerantha*). Despite these detailed studies, many later botanists, probably influenced by its very distinctive appearance when in fruit (though not in flower), have chosen to maintain the genus (e.g. Hayek, 1924, Schischkin in Komarov, 1936). The reasons for Mattfeld's view being the more correct one are discussed in full in the revision of Orient species.

Rhodalsine:

Like *Honkenya*, this group has to some extent retained the primitive broad-leaved condition, although the leaves are linear in *Minuartia vestita* and some forms of *M. geniculata*. In general facies the plants, which grow on maritime cliffs or under rather desert conditions, resemble species of *Spergularia* rather than any group of *Minuartia* and this is accentuated by their pink petals. Within the *Minuartia* affinity they are unusual in having accumbent cotyledons (a character shared only by the *Spergella* group) and more especially in the structure of the flowers, which are subperigynous, the petals and stamens arising from a short calyx tube.

The distinctiveness of the group was first recognised by Fenzl (1840) who described it as one of the divisions of "*Alsine*" (*Minuartia*); in 1845 Gay gave it generic rank under the name *Rhodalsine*. Most authors since have regarded it as a section or subgenus of *Minuartia* ("*Alsine*"), but Williams (1898a) treated it as a distinct genus—publishing a "Note Monographique" on the single polymorphic species complex then known to belong to the group.

The Somaliland species, *Arenaria vestita* Baker, is clearly referable to this group (a relationship, which so far as is known, has not previously been noted) and its floral structure, although subperigynous like the Mediterranean species, more nearly approaches the normal *Minuartia* pattern.

It has been noted that the status of *Honkenya* is likely to remain for long a subject of controversy, and the same applies to *Rhodalsine*. Its tendency to develop narrow leaves, its terminal inflorescence and its

typical capsule draw it closer to *Minuartia*, but it has the additional special features of accumbent cotyledons and superperigynous flowers with an extremely short calyx tube. Within *Arenaria* differences in cotyledon arrangement occur and the accumbent condition is also found in *Minuartia picta* and *M. formosa* (Subgenus *Spergella*), which have the typical floral structure and habit of *Minuartia*. Further evidence from cytology and floral anatomy may help in the evaluation of the status of the group which for the moment is retained within *Minuartia*, where it is treated as a subgenus.

Wilhelmsia (*Merckia*):

This monotypic group is very similar in habit to *Honkenya* and like it seems to be a relict broad-leaved representative of a primitive *Minuartia* stock. Except by those authors who treat *Arenaria* as a single genus (e.g. Fernald, 1919 and Maguire, 1951), it has always been maintained generically on account of its inflated, partially septate capsule. Mattfeld was unaware of its method of dehiscence but from the structure of the immature capsule (cf. Mattfeld 1922a) it clearly belongs to the loculicidal group. This is also the position of the partial septa (which are therefore false septa) although there are also secondary furrows along the true septal line. The capsule being rather fleshy, if it opens at all, it probably does so rather irregularly.

Were *Honkenya* to be included within *Minuartia* there would be some basis for treating *Wilhelmsia* similarly; it is, however, completely isolated from any existing group of that genus and its resemblance to *Honkenya* is almost certainly superficial.

As the name *Merckia* Cham. & Schlecht. (1826) is antedated by *Merkia* Borkh. (1792), a genus in the *Jungermanniales*, the name *Wilhelmsia* Reichb. (1828) is the correct one (cf. McNeill, 1960).

Minuartia:

Within Mattfeld's concept of *Minuartia* the distinctive groups *Honkenya*, *Hymenella* and *Rhodalsine* have already been discussed, the first named being treated as a separate genus and the last two raised to subgeneric rank (Mattfeld included each of them as sections). A fourth group of Mattfeld's *Minuartia* seems also to stand in a very isolated position; this is the group *Spergella* which superficially resembles species of *Spergula* and which is characterised by its accumbent cotyledons, falsely whorled leaves and pink flowers.

The two species have the general habit of *Minuartia* but cannot be easily related to any other group (Mattfeld's association of them with Section *Spectabiles* cannot be upheld). This distinctiveness was noted by Gay who in his manuscript notes (in the Library at Kew) proposed the generic name "*Godronia*" for the group. It is here treated as a subgenus of *Minuartia* under Fenzl's name *Spergella* (not to be confused with Reichenbach's genus *Spergella* which represents pentamerous species of *Sagina*).

It is therefore proposed, as a result of the present studies, to recognise seven genera, and although no finality can perhaps ever be achieved in so complex a group, it is hoped that by taking a wide view and segregating only such natural groups as stand out clearly, something more stable and

satisfactory has been achieved than simply a "*via media*" between the extremes of Krause (1901) and Reichenbach (1828, 1837, 1841).

The seven genera are keyed below:

KEY TO ACCEPTED GENERA

- 1a. Sepals almost completely scarious, more than twice as long as petals; stamens 5, with 5 staminodes; styles 2; capsule 4-valved, 1-seeded; flowers numerous in axillary and terminal panicles; much-branched climber with relatively large lanceolate leaves (Himalaya to Indo-China) 3. *Brachystemma*
- 1b. Sepals largely herbaceous or coriaceous, sometimes with a rather narrow scarious margin (rarely margin broad, forming most of the sepal and then petals usually as long as or longer than sepals, stamens 10, styles 3, capsule 3- or 6-valved or toothed, and inflorescence always terminal); inflorescence usually terminal or if (also) axillary usually 1-few flowered; habit various, very rarely a scrambling climber 2
- 2a. Leaves fleshy, ovate, sessile, 5-40 mm. long; capsule globose, somewhat fleshy; seeds exstrophiolate; plants spreading with ascending stems (maritime or riparian plants) 3
- 2b. Leaves various, if ovate, either thin and not at all fleshy, or else very small (< 5 mm.) and plants \pm pulvinate; capsule completely unilocular, very rarely globose, not at all fleshy; seeds reniform, or globular or flattened (< 2.5 mm.), rarely pyriform (*Arenaria* Subgenus *Eremogone*) (plants of various habitats, very rarely sea-shores or river banks) 4
- 3a. Capsule inflated, divided beyond half-way by 3 incomplete false septa, and bearing 3 secondary furrows (opening along the false septa by 3 furrowed valves—sometimes also splitting irregularly along the secondary furrows); staminal glands inconspicuous; seeds reniform, < 1.5 mm. (E. Asia and N.W. America) 5. *Wilhelmsia*
- 3b. Capsule completely unilocular, not inflated, opening by 3 unfurrowed valves; staminal glands prominent; seeds large (> 2.5 mm.), pyriform; maritime strand plants (N. Temperate and Arctic regions) 4. *Honkenya*
- 4a. Carpels 2; capsule globose, inflated, opening by 2 valves; ovules few (c. 4); seeds 2(-3) exstrophiolate; inflorescence many-flowered, axillary and terminal; petals often indented at apex (sometimes bifid); leaves relatively large and thin, lanceolate and sessile or ovate and petiolate; slender to rather robust straggling annuals (S.W. Asia to C. Asia) 7. *Lepyrodiclis*
- 4b. Carpels 3, occasionally 2; capsule ovoid to cylindrical, never inflated, opening by 3, 4 or 6 valves or teeth; petals usually entire, occasionally fimbriate or even emarginate; ovules usually many but sometimes reduced to few or one (particularly where the flowers are aggregated together or the plant is densely pulvinate); leaves usually small, often linear or subulate, if relatively large, broad and thin, then seeds usually smooth, sometimes strophiolate. 5

- 5a. Seeds smooth, shiny (rarely obscurely tuberculate), with a whitish (or brownish) oily appendage (strophiole) near the hilum; flowers 4-merous with 2 carpels or 5-merous with 3 carpels; capsule opening by twice as many valves as styles; slender-stemmed, \pm mat-forming, annuals or rhizomatous perennials (N. Temperate regions, esp. Europe) 2. *Moehringia*
- 5b. Seeds without an oily appendage (occasionally winged by the protrusion of the testa, or rarely with a small colourless testa protrusion near the hilum); flowers 5-merous, rarely 4-merous and then with 3 carpels; plants rarely (never?) rhizomatous 6
- 6a. Capsule opening by as many valves as styles; styles 3; leaves usually linear-subulate or setaceous (sometimes linear-lanceolate to lanceolate, sessile and rather rigid and then sepals \pm prominently 5-7-nerved, rarely broader, subpetiolate and then flowers subperigynous and stamens usually inserted at two levels); if sepals indurate at the base, then plants annual or sepals with prominent parallel white stripes on either side of the green median nerve (very rarely 3 nerved); inflorescence always terminal; seeds buff to very dark brown, never reddish or black (N. Hemisphere, Chile) 6. *Minuartia*
- 6b. Capsule opening by twice as many teeth or valves as styles; styles 2 or 3; leaves various often lanceolate to ovate, if rigid-setaceous, or linear and grass-like, plants perennial and sepals usually indurate at the base, 1-nerved or rather obscurely nerved but without prominent parallel white strips; stamens always uniseriate attached to a hypogynous disc; inflorescence terminal or axillary, seeds usually pale reddish-brown to black (N. Hemisphere; mts. of S. America) 1. *Arenaria*

INFRA-GENERIC CLASSIFICATION

1. *Arenaria*

Arenaria L., Sp. Pl. 423 (1753) et Gen. Pl. ed. 5, 193 (1754) (non *Arenaria* sec. Desv. in J. Bot. Desv. 3, 219 (1816)); Benth. in Benth. & Hook. f., Gen. Pl. 1, 150 (1862), pro parte; Pax & Hoffmann in Engler & Harms, Natürl. Pflanzenfam. ed. 2, 16c, 315 (1934).

Syn.: *Gypsophytum* Adans., Fam. 9, 256 (1763) ("*Gypsophyton*" in indic.) (\equiv *Arenaria* L.).*

Alsinanthus Desv. in J. Bot. Desv. 3, 221 (1816).

Arenaria Sect. *Arenarium* Ser. in DC., Prodr. 1, 401 (1824), pro parte.

Arenaria Sect. *Alsinanthus* Dumort., Florula Belg. 109 (1827) (\equiv *Alsinanthus* Desv.).

Sabulina Subgenus *Alsinanthus* (Desv.) Reichb., Fl. Germ. Excurs. 785 (1832) quoad basionom., excl. spp.

Lectotype: *A. serpyllifolia* L.—cf. Green in Hitchcock & Green (1929).

* The symbol \equiv implies nomenclatural identity (i.e. the two names are based on the same type). The symbol is frequently placed in brackets (\equiv) in front of names in synonymy which are based on the same type as the accepted name.

Key to subgenera

- 1a. Styles 2, capsule splitting by 4 valves (rarely styles 3 & capsule valves 6 in *Odontostemma*); plants diffuse 2
- 1b. Styles 3, capsule splitting by 6 valves or teeth, or occasionally 2 and capsule valves 4 and then plants densely pulvinate; petals entire or slightly retuse 3
- 2a. Calyx cuneate, sepals straight (erect, spreading at anthesis), not at all saccate, acute-acuminate, \pm strongly 3-nerved, with a very narrow membranous margin; seeds minutely tuberculate, testa not inflated; leaves linear-subulate; petals entire, about as long as the sepals; inflorescence a regular many-flowered (> 6) dichasium, bracts setaceous; slender annual (or biennial) herb (S. France)
V *Arenariastrum*
- 2b. Calyx truncate, sepals curving outwards, \pm saccate at the base obtuse; obscurely nerved with a rather broad membranous margin; seeds rough without cell-like markings, testa usually inflated; leaves linear to ovate, very rarely subulate and never setaceous; petals retuse, emarginate or fimbriate, usually longer than the sepals (but cleistogamous flowers can also occur); inflorescence various, bracts foliose with vegetative shoots arising in the inflorescence region; diffuse annual, biennial or perennial herbs (Sino-Himalaya) X *Odontostemma*
- 3a. Sepals inflexed at the apex and margins, of one texture throughout (usually coriaceous); flowers small < 5 mm., solitary, sessile or shortly stalked, enclosed by or scarcely overtopping the upper leaves which resemble the sepals in structure and often merge into them; leaves small, usually < 5 mm., subulate to ovate, imbricate, coriaceous throughout (not thickened at margins); styles frequently 2; capsule membranous, seeds usually (? always) smooth and shiny; plants densely pulvinate (C. & S. America) II *Dicranilla*
- 3b. Sepals not inflexed at the apex and margins (or only a thin membranous margin inflexed); inflorescence various, if flowers solitary and scarcely overtopping the upper leaves, then either sepals herbaceous or membranous markedly dissimilar to the very coriaceous leaves, or else flowers large and sepals and leaves both either hardened or else broadly scarious at the apex and margins; leaves various, if coriaceous then either with a scarious margin or else hardened and thickened round the margins; styles usually (? always) 3; capsule frequently coriaceous or woody 4
- 4a. Capsule cylindrical, long exserted (> twice as long as sepals), membranous, opening by 6 short teeth; seeds smooth rather shiny (with a very small tuft of white hairs at hilum); caespitose plants with ovate to lanceolate sessile leaves; flowers in 1- few-flowered terminal cymes (Pyrenees & Cantabrian mts.) III *Porphyrantha*
- 4b. Capsule ovoid, enclosed by or up to twice as long as calyx (very rarely cylindrical and then about as long as calyx), varying in texture but when membranous, usually opening up completely by valves; seeds various, not usually smooth in plants with a terminal inflorescence. 5

- 5a. Seeds smooth and shiny, without any visible markings at $\times 70$; flowers typically solitary, axillary, long-pedicelled, occasionally by the reduction of the leaves and internodes forming a terminal monochasium (bracts usually herbaceous and leaf-like, though reduced in size); leaves and sepals herbaceous not hardened at the base or apex; plants perennial (S. & C. America, extending into N. America) I *Leiosperma*
- 5b. Seeds usually with cell-like markings on the testa, the 'cells' frequently expanded forming tubercles, rarely testa without any cell-like sculpturing and then bearing numerous minute papillae or with a dull roughened surface; flowers usually in terminal and sometimes also axillary cymes or panicles and bracts usually rather membranous or scarious very different from the leaves (though frequently showing a gradual transition), occasionally flowers solitary and then only terminal (or in a few spp. terminating axillary leafy shoots); plants annual or perennial 6
- 6a. Leaves narrowly linear to ovate, herbaceous, hardened at the margins and apex (very rarely not—cf. *Solitaria*), never truly setaceous or subulate; flowers solitary or occasionally up to 3 in a cluster, terminal; sepals herbaceous indistinctly veined, not at all hardened at the base; caespitose or pulvinate plants 7
- 6b. Leaves entirely herbaceous or with a scarious margin, or else setaceous often pungent, occasionally leaves \pm ovate, tetrastichous with a prominently thickened margin, and then sepals prominently veined 8
- 7a. Sepals acute, usually hardened at the apex and margins; leaves relatively large (> 5 mm. long), ovate, acute to acuminate, \pm remote or often overlapping but never densely imbricate or tetrastichous, not or scarcely persistent; flowers always solitary, large, showy (sepals > 5 mm.; petals white to pink about twice as long as sepals); plants caespitose, sometimes densely so, but never pulvinate (Sino-Himalaya) IX *Solitaria*
- 7b. Sepals obtuse, with a membranous margin, leaves persistent, linear to linear-lanceolate or if ovate, small (< 5 mm.) and densely imbricate or tetrastichous; flowers small, or if rather large, leaves linear to linear-lanceolate; plants usually densely pulvinate (rarely somewhat caespitose and leaves not very persistent, and then leaves linear and flowers frequently in clusters of 3) (Sino-Himalaya) VIII *Dolophragma*
- 8a. Sepals usually lanceolate to linear-lanceolate, long acuminate (rarely broader and acute and then plants densely pulvinate and flowers subsessile), somewhat hardened at the base, with 1-3 prominent nerves near the centre and a relatively broad scarious margin; leaves subulate to linear with a distinct scarious margin, never long and grass-like and never strictly setaceous; flowers often solitary shortly stalked or inflorescence a long-stalked terminal cluster; plants densely caespitose to densely pulvinate (leaves always persistent) (Sino-Himalaya & W.N. America) VI *Eremogoneastrum*

- 8b. Sepals various, rarely with a broad scarious margin and then individual nerves not prominent or leaves strictly setaceous or long and grass-like; leaves various, never markedly scarious-margined (very rarely minutely so) 9
- 9a. Sepals markedly hardened at the base, often the receptacle and entire lower part of the calyx becoming ligneous in fruit, rarely only somewhat hardened and then leaves pungent; cotyledons usually accumbent; leaves long linear and grass-like or short strictly setaceous or pungent, never broad or flaccid; inflorescence a terminal cyme or panicle of cymes, occasionally contracted into a head or a number of cymose clusters, rarely reduced to a single flower; plants perennial, often stoutly caudiculate (E. Asia and W.N. America) VII *Eremogone*
- 9b. Sepals not or scarcely hardened at the base; cotyledons incumbent; leaves usually lanceolate to ovate, herbaceous or occasionally coriaceous, sometimes linear-subulate and then always flaccid; inflorescence various, sometimes reduced to 1-3 flowers, occasionally axillary as well as terminal; plants annual or perennial

IV *Arenaria*

I. Subgenus *Leiosperma* McNeill, **nom. et stat. nov.**: Sect. *Leiospermae* Williams.

Syn.: *Spergulastrum* Michx., Fl. Bor. Amer. 1, 275 (1803), pro parte (parte altera = *Stellaria*).

Arenaria Sect. *Leiospermae* Williams in Bull. Herb. Boiss. 3, 600 (1895).

Type: *A. musciformis* Triana & Planch. in Ann. Sci. Nat. sér. 4, 17, 150 (1862).

Other species:

Except in the case of Orient plants, there has been no thorough assessment of the status of the species cited. In general these lists comprise the species recognised by Williams (1898) or Mattfeld (1922), names not included in their revisions (mostly published since) and widely used synonyms. Names of species of which type material has been examined are preceded by an exclamation mark—!; the exclamation mark in brackets (!), indicates that only a photograph of the type has been seen.

A. achalensis Griseb. (1879)

A. alsinoides Willd. ex Schlecht. (1813)

! *A. bourgaei* Hemsley (1879)

A. catamarcensis Pax (1893)

? *A. crassipes* Baehni & Macbride (1937)

A. decussata Willd. ex Schlecht. (1813)

A. guatemalensis Standley & Steyerl. (1944)

A. jamesoniana Rohrb. (1872)

A. lanuginosa (Michx.) Rohrb. (1872)

A. lycopodioides Willd. ex Schlecht. (1813)

A. mandoniana Wedd. (1864)

A. megalantha (Rohrb.) Williams (1898)

A. microphylla Phil. (1856)

A. muscoides Kunth (1823) (= *A. nana*)

A. nana Willd. ex Schlecht. (1813)

? *A. nitida* (Bartl.) Rohrb. (1872)

A. orbignyana Wedd. (1864)

A. paludicola Robinson (1897)

A. palustris Naud. in C. Gay (1845), non S. Wats. (1876)

! *A. parvifolia* Benth. (1845)

A. peyritschii Rohrb. (1872)

A. pleurantha Phil. (1893)

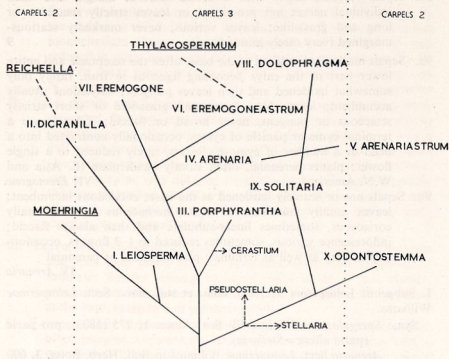


FIG. 1. Diagram of the probable inter-relationships and evolution of the subgenera of *Arenaria*.

A. poeppigiana Rohrb. (1872)

! *A. reptans* Hemsley (1879)

A. rohrbachiana Garcke (1872)

A. saxosa A. Gray (1851)

A. serpens Kunth (1823)

A. soratensis Rohrb. (1872)

*Excluded species:

! *A. andina* Rohrb.—not *Arenaria* (possibly *Minuartia* sp.)

A. standleyi Baehni & Macbride (1937)

A. stuebelii Hieron. (1895)

A. tetragyna Willd. ex Schlecht. (1813)

A. venezuela Briq. (1911)

The subgenus *Leiosperma* with smooth shiny seeds, usually axillary flowers and entirely herbaceous sepals, is confined to the New World, and has its great centre of diversity in the Andes. It is regarded as a relatively primitive group within the genus, to a large extent paralleling the predominantly old world Subgenus *Arenaria*. *Leiosperma* appears to have given rise to the highly evolved Subgenus *Dicranilla*. Probably all the South and Central American species of *Arenaria* belong to one or other of these two subgenera (mostly *Leiosperma*), and it is difficult with the material available to draw the dividing line between them. The genus *Moehringia*, characterised by a strophiolate seed, also shows a close affinity with *Leiosperma* and they have possibly evolved from a common ancestral type (cf. Figs. 1 and 2).

* Additional excluded species not included in these lists can be traced through the index which will follow the second paper of the series.

Special references: Hauman & Irigoyen (1923), Macbride (1937), Reiche (1895), Rohrbach (1872), Standley & Steyermark (1946), Steyermark (1951).

II. Subgenus *Dicranilla* (Fenzl) Williams in Bull. Herb. Boiss. 3, 599, 602 (1895).

Syn.: *Arenaria* c. *Dicranilla* Fenzl in Endlicher, Gen. Pl. 967 (1840).
Dicranilla (Fenzl) Reichb., Repert. Herb. Nomencl. 205 (1841).
Arenaria Sect. *Dicranilla* (Fenzl) Pax in Engler & Prantl, Natürl. Pflanzenfam. 3(1b), 84 (1889).

Arenaria Sectiones *Radianes*, *Pycnophyllae* & *Pedunculosae* Williams 1. c. 602 (1895).

Lectotype: *A. dicranoides* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Spec. 6, 34 (1823) (= *Lobelia bryoides* Willd. ex Roem. & Schult. (1819), non *A. bryoides* Willd. ex Schlecht. (1813)).

Other species:

<i>A. alpamarcae</i> A. Gray (1857)	<i>A. moritziana</i> Pax (1893)
<i>A. aphanantha</i> Wedd. (1864)	? <i>A. nitida</i> (Bartl.) Rohrb. (1872)
<i>A. bisulca</i> (Bartl.) Rohrb. (1872)	<i>A. pedunculosa</i> Wedd. (1864)
<i>A. boliviana</i> Williams (1898)	<i>A. pycnophylla</i> Rohrb. (1872)
(= <i>conferta</i> Wedd. non Boiss.)	<i>A. pycnophylloides</i> Pax (1893)
<i>A. bryoides</i> Willd. ex Schlecht. (1813) (paratype species)	! <i>A. radians</i> Benth. (1845)

A subgenus of about 12 species confined to the high Andes of South America and the mountains of Mexico and Central America. The species appear to be specialised alpine derivatives of species such as *A. decussata* and *A. lycopodioides* in Subgenus *Leiosperma* (cf. figs. 1 and 2).

Special references: Hauman & Irigoyen (1923), Macbride (1937), Rohrbach (1872).

III. Subgenus *Porphyrantha* (Fenzl) McNeill, stat. nov.

Syn.: *Dufourea* Grenier in Act. Soc. Linn. Bord. 9, 25 (1837) pro parte, non Bory ex Willd. (1810), nec Kunth (1818).

Arenaria c. *Porphyrantha* Fenzl in Endlicher, Gen. Pl. 967 (1840).
Porphyrantha (Fenzl) Reichb., Repert. Herb. Nomencl. 205 (1841).

Arenaria Sect. *Porphyrantha* (Fenzl) Grenier & Godron, Fl. Fr. 1, 262 (1848) ('*Porphyrantha*').

Type: *A. purpurascens* Ram. ex DC., Fl. Fr. 4, 785 (1805).

Syn.: *A. cerastioides* Pers. (1805), non Poir. (1789).

Excluded species:

A. cerastifolia Ram. ex DC. = *Minuartia cerastifolia* (DC.) Graebn.

A monotypic subgenus confined to the Pyrenees and the Cantabrian Mountains (fig. 2). In habit *A. purpurascens* resembles members of *Minuartia* Section *Lanceolatae* but holds a very isolated taxonomic position. The long cylindrical capsule, resembling that of *Cerastium* spp., is not found elsewhere in the *Arenaria* group, but in having entire petals, three carpels and six capsule teeth the species is a typical *Arenaria*. The inflorescence form and sepal structure resemble Subgenus *Arenaria* but the smooth shiny seeds with a tuft of white hairs at the hilum suggest that this resemblance is a superficial one. Subgenus *Porphyrantha* possibly

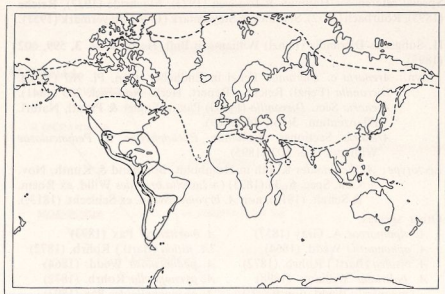


FIG. 2. Geographical distribution of subgenera of *Arenaria*.

— Leiosperma

..... Porphyrantha

--- Dicranilla

----- Arenaria

represents an early offshoot from the *Stellariineae* stock, paralleling *Cerastium* but showing a greater reduction of the gynoeceum and lacking the divided petals (cf. figs. 1 and 2).

Special references: Coste (1901), Rouy & Foucaud (1896), Willkomm & Lange (1878).

IV. Subgenus *Arenaria*

Syn.: *Arenaria* b. *Euthalia* Fenzl in Endlicher, Gen. Pl. 967 (1840).

Arenaria Subgenus *Euthalia* (Fenzl) Fenzl in Ledebour, Fl. Ross. 1, 368 (1842).

Arenaria Sect. *Euthalia* (Fenzl) Grenier & Godron, Fl. Fr. 1, 257 (1848).

Euthalia (Fenzl) Rupr., Fl. Cauc. 220 (1869).

Arenaria Subgenus *Pentadenaria* Section *Rariflorae* Williams in Bull. Herb. Boiss. 3, 602 (1895), pro parte (Subsection 3)—spec. typ. *A. ciliata* incl.

Subgenus *Arenaria* is centred in Europe and the Eastern Mediterranean with the Panarctic Section *Rariflorae* in Greenland, Canada and Alaska and one species (*A. benthamii*—Section *Arenaria*) in Texas and New Mexico; other species occur in North Africa and Central Asia and one is to be found in the mountains of East Africa (*A. foliacea*) (fig. 2). *A. serpyllifolia* and *A. leptoclados* have been introduced into North America and Australasia.

Special references: Graebner (1916), Nyman (1878), Reichenbach (1842), Willkomm (1855–56), Willkomm & Lange (1878).

Key to Sections and Series

- 1a. Plants perennial, bearing sterile leafy shoots in addition to flowering stems 2
- 1b. Plants annual, without sterile leafy shoots 11
- 2a. Leaves strongly 3-nerved, the lateral nerves marginal; sepals with a prominent median nerve 3
- 2b. Leaves with indistinct vasculature or more usually with a prominent median nerve sometimes giving rise to a number of weak lateral nerves but with no distinct marginal vasculature 4
- 3a. Leaves linear to ovate, cuneate; flowers in a lax cymose inflorescence (pedicels 5-50 mm. long); sepals with numerous indistinct lateral nerves, often keeled, markedly different from the bracts (C. Europe, E. & W. Mediterranean) B. Sect. *Grandiflorae*
- 3b. Leaves triangular (sometimes narrowly so), \pm truncate at the base; flowers in clusters (usually a terminal head), or solitary, closely invested by sheathing bracts (pedicels < 2 mm.); sepals with 2-3 pairs of rather prominent lateral nerves, the outer bract-like with prominent marginal vasculature (Spain & N. Africa) C. Sect. *Plinthine*
- 4a. Leaves obovate to orbicular with a rounded apex; seeds obscurely reticulate, the testa 'cells' not tuberculiform; testa 'cells' with a number of minute puncta ('punctate'), but no central papilla ('epapillose'); petals ovate \pm abruptly contracted at the base; inflorescence frequently axillary (S. & C. Europe, Orient, E. to India) D. Sect. *Rotundifoliae*
- 4b. Leaves linear to ovate, apex acute to obtuse (rarely broadly ovate and then apex acute); seeds various, often rugulose or tuberculate, papillose; petals usually lanceolate to obovate, cuneate at the base 5
- 5a. Sepals with a broad \pm scarious margin becoming very slightly hardened in fruit; inflorescence 8-12 flowered, very lax; seeds strongly compressed, winged, buff; cotyledons longitudinally grooved or folded away from the radicle; leaves broadly linear to linear-lanceolate \pm sessile L. Sect. *Compressae*
- 5b. Sepals with a rather narrow membranous margin, not at all hardened; inflorescence various, if very lax usually very few flowered; seeds \pm reniform, wingless, usually black; cotyledons not grooved or folded 6
- 6a. Sepals obscurely nerved or with a median nerve (often prominent) and sometimes with 1-2 pairs of laterals, always less prominent than the median nerve and usually indistinct; leaves often sessile 7
- 6b. Sepals \pm equally 3-7(-9)-nerved, the nerves distinct (or obscure in densely pubescent sepals); basal leaves usually ovate to ovate-lanceolate, petiolate; stem leaves often similar; plants \pm mat-like (E. Mediterranean, Italy & Spain) F. Sect. *Orientales* 8
- 7a. Sepals large (> 5 mm.), obscurely nerved or with a single median nerve but not at all keeled; leaves large, 15-35 mm. long; plants mat-like or ascending (S. France, Spain & Portugal) E. Sect. *Planosepalae*

- 7b. Sepals small (< 5 mm.) with a median nerve, often prominent (& sepals almost keeled) and one or two pairs of less distinct lateral nerves: leaves small 2-7 mm. long; plants caespitose often with woody caudex & caudiculi (Panarctic, Mts. of C. & S. Europe & S.W. Asia) A. Sect. *Rariflorae*
- 7c. Sepals small (< 5 mm.), obscurely nerved (actually with a number of \pm equal parallel nerves); leaves usually large, 6-15 mm. long; plants mat-like (Italy & E. Mediterranean)
- F. (i). Sect. *Orientalis* Ser. *Anomalae*
- 8a. Seeds rugulose to tuberculate, testa 'cells' with a prominent central or sub-central papilla ('papillose'); basal leaves always petiolate, usually ovate-lanceolate 9
- 8b. Seeds obscurely reticulate, or with a broad fimbriate margin, testa cells with minute puncta ('punctate'), with or without a central papilla; basal leaves ovate-lanceolate to orbicular, petiolate, or linear to lanceolate, sessile (Italy & E. Mediterranean)
- F. (i). Ser. *Anomalae*
- 9a. Stem leaves ovate to ovate-lanceolate; petals cuneate at the base 10
- 9b. Stem leaves linear-lanceolate, shortly petiolate; petals abruptly contracted at the base (Spain) F. (iv). Ser. *Hispidae*
- 10a. Upper leaves sessile, lower shortly petiolate; seeds large (0.8-1.0 mm. \times 0.6-0.7 mm.) (Bulgaria & Greece) F. (ii). Ser. *Graecae*
- 10b. All leaves gradually narrowing at the base into a petiole, that of the lower leaves almost as long as the lamina; seeds small (0.5-0.7 mm. \times 0.4-0.6 mm.) (Aegean Is., Turkey, Levant & Sinai)
- F. (iii). Ser. *Deflexae*
- 11a. Plants robust (15-25 cm. tall, stems 1.0-2.0 mm. diam.), with large linear-lanceolate to ovate leaves (18-25 mm. long); sepals large (> 4 mm. long) (Spain & N. Africa) J. Sect. *Africanae* 12
- 11b. Plants slender to rather robust (2-15 cm. tall, stems 0.25-1.0 mm. diam.), with small leaves (usually < 8 mm. long); sepals small, 2-4(-5) mm. long 13
- 12a. Seeds reniform rugulose, with distinct 'cells'; inflorescence generally dichasial (Algeria, Tunisia) J. (i). Ser. *Africanae*
- 12b. Seeds lenticular smooth, the testa without cell-like markings (i.e. as in S.-G. *Leiosperma*) but bearing minute papillae; inflorescence usually monochasial (Spain, Morocco) J. (ii). Ser. *Papillosperrmae*
- 13a. Sepals strongly 3-nerved (as in *Minuartia* Section *Sabulina*) without any subsidiary nerves; pedicels spreading or reflexed; petals much longer than sepals ("Mesopotamia") G. Sect. *Pseudosabulina*
- 13b. Sepals with a single median nerve or with a number (> 3) of nerves varying in their degree of prominence; pedicels erect or spreading; (occasionally sepals prominently 3-nerved with very weak additional nerves and then petals about as long as sepals) 14
- 14a. Adult leaves (i.e. except the first few pairs of seeding leaves) sessile, usually multinerved; petals usually much shorter than the sepals (rarely as long) (Eurasia) K. Sect. *Arenaria* 15
- 14b. All the leaves with a single median nerve, either linear or ovate, petiolate; petals as long as or longer than sepals 17

- 15a. Capsule narrowly cylindrical (> 3 times as long as broad); sepals lanceolate (3-3.5 times as long as broad), narrowly acuminate; plants rather xerophytic (Greece) K. (iii). Ser. *Cylindricae*
- 15b. Capsule conical to globose (1-2.5 times as long as broad); sepals ovate to lanceolate (1.5-3 times as long as broad), acute to acuminate 16
- 16a. Plants very xerophytic; leaves and sepals densely glandular pubescent prominently nerved; upper leaves spatulate, the nerves all alike (Crete, Cyprus & Turkey) K. (ii). Ser. *Saponarioides*
- 16b. Plants mesophytic; leaves and sepals not prominently nerved or with a prominent median nerve and less distinct lateral branches; upper leaves broadly ovate, triangular, or linear lanceolate (Eurasia, introduced in N. America & Australia) K. (i). Ser. *Arenaria*
- 17a. Upper leaves linear-subulate, lower narrowly spatulate; sepals obtuse or acute; seeds often with minute puncta on the testa 'cells' ('punctate'), papillae absent (except in *A. obtusiflora*) (Spain & N. Africa) H. Sect. *Occidentales*
- 17b. Leaf blades lanceolate to orbicular 18
- 18a. Leaves lanceolate to ovate-lanceolate, gradually narrowing into a very short petiole (or sessile); sepals with a distinct median nerve and 1 pair of less prominent lateral nerves; seeds rugulose, 'cells' punctate, epapillose (N. Europe, etc.) A. Sect. *Rariflorae*
- 18b. Leaf blades ovate-lanceolate to orbicular, lower leaves long petiolate, if upper shortly petiolate then blade \pm abruptly contracted at base; sepals with a number (5-9) of \pm equally distinct parallel nerves (median sometimes rather more prominent); seeds rugulose to sharply tuberculate, 'cells' papillose but not punctate (E. Mediterranean, Spain) F. (v). Sect. *Orientalis* Ser. *Orientalis*

A. Sectio *Rariflorae* Williams in Bull. Herb. Boiss. 3, 602 (1895), pro parte, non Divisio "*Rariflorae*" Fenzl (1842), nomen invalidum.

Syn.: *Arenaria* Subgenus *Euthalia* Series "*Humifusae*" Schischk. in Komarov, Fl. U.R.S.S. 6, 537 (1936)—descr. rossice.

Perennial caespitose plants, rarely annual, often with woody caudex and caudiculi. *Leaves* (linear to) lanceolate to ovate-spatulate, sessile but cuneate, or very shortly petiolate, bearing a median nerve and sometimes lateral branches; apex acute to obtuse. *Inflorescence* terminal (rarely a few lateral) bearing 1-5(-9) flowers; bracts narrowly triangular or subulate. *Sepals* \pm acute with a prominent median nerve and 1-3 pairs of inconspicuous lateral nerves (sometimes rather prominent at the base of the sepal). *Petals* oblanceolate to ovate, long attenuate to obtusely cuneate, longer than the sepals. *Seeds* \pm obscurely reticulate punctate not papillose.

Type species: *A. ciliata* L., Sp. Pl. 423 (1753).

Other species:

- | | |
|--|--|
| ! <i>A. antitaurica</i> McNeill (1961) | ? <i>A. chamissonis</i> Maguire (1951) |
| ! <i>A. bulica</i> Stapf ex Williams (1898). | <i>A. cinerea</i> DC. (1815) |
| | ! <i>A. cretica</i> Spreng. (1825) |

- | | |
|---|--|
| <i>A. gothica</i> Fries (1839) | <i>A. norvegica</i> Gunn (1772) |
| <i>A. gracilis</i> Waldst. & Kit. (1812) | <i>A. pseudofrigida</i> (Ostenf. & Dahl) |
| <i>A. humifusa</i> (Swartz) Wahlb. (1812) | Juz. ex Schischk. (1936) |
| ! <i>A. huteri</i> Kern. (1872) | <i>A. redowskii</i> Cham. & Schlecht. |
| ! <i>A. minutissima</i> Rech. & Esfand. | (1826) |
| (1951) | ! <i>A. uninervia</i> McNeill (1961) |

Section *Rariflorae* is a widely distributed Arctic-Alpine group occurring throughout the northernmost parts of Europe and America and extending south into the mountains of C. Europe, Spain, the Balkans, Anatolia and Iran. The Oriental and East European species may form a recognisable group within the section, while the Spanish species (*A. cinerea*) is rather doubtfully referred to this section and should perhaps be placed in a group of its own.

The present circumscription is much more restricted than that of Williams, who applied the name to all those members of his Subgenus *Pentadenaria* in which the inflorescence was lax, probably taking the name from Fenzl's use of it (in Ledebour, *Flora Rossica*) in Subgenus *Eremogone*. (*Pentadenaria* Williams being composed partly of species in Subgen. *Arenaria* and partly of ones in Subgen. *Eremogone*). Fenzl's name is invalid in being ranked as a 'Divisio' and has thus no nomenclatural status whatsoever (and cannot be considered as an earlier homonym). Williams makes no direct reference to Fenzl, gives a description and cites *A. ciliata* as the exemplary species; despite its rather confused use, his name must therefore be adopted.

B. Sectio *Grandiflorae* McNeill, sect. nov.

Plantae perennes, caespitosae vel tegetiformes; caudex et caudiculi lignosi plerumque prominentes. *Folia* ovato-lanceolata vel linearia, acuta \pm sessilia, nervis tribus prominentibus (una mediana, duabus marginalibus) praedita. *Inflorescentia* terminalia 1-8-floribus instructa. *Sepala* ovata vel lanceolata, acuta vel acuminata, nervo mediano prominentissimo (aliquanto sepalis carinatis) et nervis lateralibus 2-6 distinctis praedita. *Petala* ovata vel oblanceolata, cuneata vel attenuata, sepalis excedentia.

Type: *A. grandiflora* L., Syst. Pl. ed. 10, 1034 (1759).

Other species:

- | | |
|---------------------------------------|-------------------------------------|
| ! <i>A. bourgeana</i> Coss. ex Willk. | ! <i>A. kotschyana</i> Fenzl (1843) |
| (1876) | ! <i>A. tmolea</i> Boiss. (1842) |
| <i>A. incrassata</i> Lange (1864) | <i>A. triflora</i> L. (1771) |

Section *Grandiflorae*, which is closely related to Section *Rariflorae*, comprises two species complexes, one in S.W. and C. Europe and one in Turkey.

C. Sectio *Plinthine* (Reichb.) McNeill, stat. nov.

- Syn.: *Arenaria* c. *Plinthine* Reichb., Fl. Germ. Excurs. 792 (1832).
Plinthine (Reichb.) Reichb., Handb. 298 (1837).

Type: *A. aggregata* (L.) Lois. in G. F. Curier (ed.), Dict. Sci. Nat. 46, 513 (1827) et Fl. Gall. ed. 2, 1, 317 (1828).

Other species:

- | | |
|---|--|
| <i>A. armerina</i> Bory (1820) | <i>A. querioides</i> Pourr. ex Willk. (1847) |
| <i>A. capitata</i> Lam. (1778) | |
| <i>A. erinacea</i> Boiss. (1839-45) | <i>A. racemosa</i> Willk. (1847) |
| <i>A. lithops</i> Heywood* | <i>A. tetraquetra</i> L. (1753) |
| <i>A. pseudarmeriastrum</i> Rouy (1882) | <i>A. tomentosa</i> Willk. (1852) |

Section *Plinthine* is a very distinctive group of plants endemic to the Iberian Peninsula and North Africa; its members appear to be highly evolved derivatives of Section *Grandiflorae*.

Special reference: Font Quer (1948).

D. Sectio *Rotundifoliae* McNeill, sect. nov.

Syn.: *Arenaria* Subgenus *Euthalia* Series "*Rotundifoliae*" Schischkin in Komarov, Fl. U.R.S.S. 6, 538 (1936)—descr. rossice.

Plantae perennes (?vel rarissime annuae) tegetiformes. *Caules* longi foliati, inflorescentiae laterales et interdum terminales gerentes. *Folia* ovata vel orbiculata, breviter petiolata, uninervia, apice subrotundata vel late obtuso. *Flores* graciles. *Sepala* acuta vel obtusa nervo mediano distincto et nervis lateralibus 4-6 indistinctis praedita. *Petala* ovato-lanceolata vel orbiculata, ad radicem obtusa vel abrupte contracta, sepalis breviora vel longiora. *Semina* obscure reticulata; 'cellulae' punctatae, epapillosae. *Type*: !*A. rotundifolia* M. Bieb., Fl. Taur. Cauc. 1, 314 (1808).

Other species:

- | | |
|---|--|
| ! <i>A. balansae</i> Boiss. (1867) | <i>A. orbicularis</i> Vis. (1850) |
| <i>A. balearica</i> L. (1768) | <i>A. orbiculata</i> Royle ex Edgew. & Hook. f. (1874) |
| <i>A. biflora</i> L. (1767) | |
| <i>A. gayana</i> Williams (1898) | <i>A. ovalifolia</i> Somm. & Lev. (1893) |
| ! <i>A. halacsyi</i> Bald. (1891) | <i>A. tenella</i> Duthie ex Williams (1898) |
| <i>A. neelgherrense</i> Wight & Arn. (1834) | <i>A. turkestanica</i> Schischk. (1937) |

With their characteristic creeping habit and rather round leaves, the members of Section *Rotundifoliae* are usually readily distinguished. *A. balearica*, in which the flowers are solitary on long pedicels and the sepals obtuse, stands apart from the other members of the Section. The group as a whole appears to lie intermediate between Section *Rariflorae* on the one hand and Section *Planosepalae* and Section *Orientales* Series *Anomalae* on the other.

E. Sectio *Planosepalae* McNeill, sect. nov.

Plantae perennes laxae tegetiformes vel ascendentes. *Folia* magna (15-35 mm.), linearia vel ovata, uninervia, sessilia. *Inflorescentia* terminalia, 1-10-floribus instructa; bractae foliaceae sed foliis multo parviores. *Flores* magni. *Sepala* 6-10 mm. longa, vena mediana non prominente praedita. *Petala* sepalis multo longiora. *Semina* tuberculata. *Type*: *A. montana* L., Cent. Pl. 1, 12 (1755).

A. montana, the single species of the section, is confined to the Iberian peninsula and South-west France and appears to be taxonomically rather isolated. Its closest affinity is possibly with species such as *A. bertolonii* in Section *Orientales* Series *Anomalae*.

* *A. lithops* Heywood, nom. nov.: *A. pulvinata* Huter in Öst. Bot. Zeitschr. 54, 450 (1904), non Edgew. (1874).

F. Sectio Orientales McNeill, sect. nov.

Plantae perennes vel annuae, caespitosae vel tegetiformes vel graciles, numquam caudice et caudiculis crassis lignosis praeditae. *Folia* radicalia plerumque ovata vel ovato-lanceolata, petiolata, acuta, uninervia vel nervis lateralibus inconspicuis etiam praedita; folia caulina varia saepe ovata petiolata, semper vena mediana tantum conspicua. *Inflorescentia* terminalia plerumque multiflora. *Sepala* ad 5 mm. longa, plurinervia; vena mediana venis lateralibus vix prominentior sed plerumque venae omnes \pm distinctae (praeter in sepalis pilosissimis). *Petala* sepalis plerumque paulo vel multo longiora. *Semina* saepe subtiliter tuberculata, papillosa. *Type*: *A. pamphylica* Boiss. & Heldr. in Boiss., Diagn. Pl. Orient. ser. 1, 8, 102 (1849)

In Section *Orientales* both the annual and perennial habits are well developed, although the perennial plants lack a woody base and are probably relatively short-lived. Of the perennial series, *Graecae* is closest to Section *Rariflorae* while Series *Deflexae* appears in most respects intermediate between Series *Graecae* and the annual *Orientales* s.s. Series *Hispidae* would seem to be a linear-leaved group paralleling the *Deflexae* in the W. Mediterranean. Series *Anomaliae* is placed within the section because of the general habit and flower structure of its members but is a rather heterogeneous group which shows affinity with Sections *Rotundifoliae* and *Planosepalae*.

The centre of distribution of the section is the Eastern Mediterranean area but Series *Hispidae* is a West European group, Series *Anomaliae* has an Italian species (*A. bertolonii*) and Series *Orientales* has one species in Spain (*A. retusa*).

F. (i). Series Anomaliae McNeill, ser. nov.

Plantae perennes, saepe tegetiformes. *Folia* varia (interdum linearia sessilia). *Sepala* plurinervia; venae saepe obscurae. *Inflorescentia* plerumque pauciflora; bracteae plerumque foliaceae; pedicelli saepe longi erecti vel patentes. *Semina* obscure reticulata, punctata raro etiam papillosa.

Type: *A. sipylea* Boiss., Diagn. Pl. Orient. ser. 1, 1, 52 (1842).

Other species:

A. angustifolia McNeill (1961)

A. libanotica Boiss. (1867)

(incl. *A. adonidis* Post, 1896)

A. bertolonii Fiori & Paol.

A. saxifraga (Bertol.) Fenzl

(1896-98)

(1848) (\equiv *A. bertolonii*)

A. speluncarum McNeill (1961)

F. (ii). Series Graecae McNeill, ser. nov.

Plantae perennes caespitosae vel \pm tegetiformes. *Folia* radicalia ovata vel ovato-lanceolata, breviter petiolata; folia caulina ovata vel lanceolata, sessilia. *Inflorescentia* pauciflora; bracteae foliaceae. *Petala* sepalis longiora. *Semina* 0.8-1 mm. longa \times 0.6-0.7 mm. lata.

Type: *A. graeca* (Boiss.) Halácsy, Consp. Fl. Graec. 1, 232 (1900) (\equiv *A. filicaulis* ssp. *graeca* (Boiss.) McNeill ined.).

Species:

A. filicaulis Fenzl (1843)

?*A. pirinica* Stoj. (1941)

(incl. type).

A. teddi Turrill (1936)

F. (iii). Series Deflexae McNeill, ser. nov.

Plantae perennes \pm tegetiformes. *Folia* ovata vel ovato-lanceolata, petiolata (radicalia longe petiolata). *Inflorescentia* pauci vel multiflora; bractae subulatae. *Petala* cuneata, sepalis paulo (vel multo) longiora. *Semina* 0.5–0.7 mm. longa \times 0.4–0.6 mm. lata.

Type: *A. deflexa* Decaisne, *Florula sinaica* 53 (1834) (reprint from *Ann. Sci. Nat.* ser. 2, 3, 277).

Other species: *A. fragillima* Rech. f. (1939).

F. (iv). Series Hispidae McNeill, ser. nov.

Plantae caespitosae vel tegetiformes. *Folia* radicalia ovata vel ovato-lanceolata, longe petiolata; folia caulina lineari-lanceolata vel subulata, vena mediana subprominente venis lateralibus obscuris non marginalibus praedita. *Petala* ad basim in unguem abrupte contracta, sepalis longiora. *Type*: *A. hispida* L., *Sp. Pl.* 425 (1753).

Other species:

A. ligericina Lecoq. & Lam. (1847) (= *A. lesurina* Loret (1862)).

F. (v). Series Orientales

Plantae annuae; Characteres ceteri instar *Seriei Deflexae* sed bractae foliaceae vel subulatae nec semper subulatae.

Species:

! *A. kurdica* McNeill (1961)

A. oxypetala Sibth. & Sm. (1806)

! *A. luschanii* McNeill*

! *A. pamphylica* Boiss. & Heldr. (1849) (type)

! *A. muralis* (Link) Sieber ex Spreng. (1825)

A. retusa Boiss. (1839–45)

! *A. rhodia* Boiss. (1842)

G. Sectio Pseudosabulina McNeill, sect. nov.

Planta annua, gracilis. *Folia* lineari-subulata flaccida. *Inflorescentia* magna effusa, multiflora; bractae subulatae; pedicelli patentes vel deflexi. *Sepala* acuta, prominentissime trinervia (nervis aliis nullis). *Petala* oblongo-spatulata sepalis multo (fere duplo) longiora. *Capsula* subglobosa calyce subaequans vel paulo brevior. *Semina* subtiliter tuberculata, papillosa.

Type: *A. sabulina* Grisebach ex Fenzl, *Illustr. Pl. Syr. Taur.* 47 (1843).

The single species of Section *Pseudosabulina* is confined to the semi-desert region on the borders of Turkey, Syria and Iraq. The Section shows a strong superficial resemblance to *Minuartia* Section *Sabulina* (particularly in the sepal structure) but its true affinities lie with *Arenaria* Section *Orientales* Series *Orientales* (particularly *A. kurdica*).

H. Sectio Occidentales McNeill, sect. nov.

Plantae annuae graciles et humiles, 5–10(–15) cm. altae. *Folia* uninervia, < 8 mm. longa, saepe subcarnosa; radicalia lineari-subulata vel anguste spatulata; caulina lineari vel lineari-subulata. *Inflorescentia* dichasia multiflora effusa. *Sepala* acuta vel obtusissima, nervis obscuris vel paucis (c. 3) subprominentis praedita. *Petala* sepalis multo longiora. *Semina*

* *A. luschanii* McNeill, *nom. nov.*: *A. pusilla* Stapf in *Denkschr. Acad. Wiss., Wien* 51: 355 (1896), non S. Wats. (1881–82).

reniformia, obscure reticulata, saepe punctata rarissime papillosa (*A. obtusiflora*).

Type: *A. conimbricensis* Brot., Fl. Lusit. 2, 200 (1804).

Other species:

! *A. algarbiensis* Welw. ex Willk. (1853)

! *A. capillipes* (Boiss.) Boiss. (1839-45)

A. ciliaris Loscos (1876)

A. conica Boiss. (1839-45)

A. controversa Boiss. (1839-45)

A. emarginata Brot. (1804) (incl.

A. sordida Chaub. (1838))

! *A. loscosii* Texid. (1877)

A. modesta Duf. (1820)

! *A. obtusiflora* Kunze (1846)

! *A. tenuis* Gay (1867)

The linear to subulate leaved Section *Occidentales* parallels in the Western Mediterranean the annual, ovate to ovate-lanceolate leaved Section *Orientales* Series *Orientales*, which is predominantly an Eastern Mediterranean group. Section *Occidentales* differs further in usually having punctate and not papillose seeds and probably represents an independent line of development of the annual habit.

The Section could probably be subdivided into a group with obtuse sepals (*A. ciliaris*, *A. conimbricensis*, *A. loscosii* and *A. obtusiflora*) and another with acute sepals. Within this second group there is some variation in the degree of prominence of the sepal nerves, species such as *A. algarbiensis* and *A. capillipes* having three prominent nerves, reminiscent of Section *Pseudosabulina*, but with subsidiary nerves also present.

J. Sectio *Africanæ* McNeill, sect. nov.

Plantæ annuæ robustæ, ex toto glanduloso-pubescentes. *Folia* radicalia 10-25 mm. longa, \pm spatulata, saepe longe petiolata; *folia* caulina 8-20 mm. longa, ovata vel lineari-lanceolata, \pm spatulata, breviter petiolata vel subsessilia. *Inflorescentia* effusa multiflora. *Sepala* magna 4-7 mm. longa, plurinervia. *Petala* spatulata sepalis multo longiora.

Type: *A. cerastioides* Poir., Voy. Barb. 2, 166 (1789).

Section *Africanæ* comprises a small group of Spanish and North African plants which are very uniform in habit and general appearance. They exhibit, however, a remarkable discontinuity in seed structure, the Spanish and Moroccan *A. hispanica* having dull black lenticular seeds rather like *Moehringia* or *Arenaria* Subgenus *Leiosperma*. They differ from these groups, however, in the dull, not shiny, testa covered with numerous minute papillae. The plants from Algeria and Tunisia now placed in Series *Africanæ* on the other hand have seeds of the type normally found in Subgenus *Arenaria*. Nothing resembling the testa structure of *A. hispanica* has been seen (except for *Moehringia* and Subgen. *Leiosperma*) and on this normally distinctive character, the species stands in a very isolated position. The resemblance to *A. cerastioides* in both vegetative and floral characters is so strong as to make any claim of convergent evolution difficult to substantiate; for this reason *A. hispanica* is included as a separate Series within Section *Africanæ*.

J. (i). Series *Africanæ*

Inflorescentia plerumque dichasialis. *Semina* reniformia, obscure reticulata, punctata.

Species:

- | | |
|---|---------------------------------------|
| <i>A. cerastioides</i> Poir. (1789) (type | <i>A. olloixii</i> Jahandiez, Maire & |
| incl. <i>A. spathulata</i> Desf. (sensu | Weiller (1931) |
| stricto) (1798). | <i>A. pomeli</i> Munby (1864) |

J. (ii). Series Papillospermae McNeill, ser. nov.

A serie typica inflorescentia plerumque monochasialis seminibus laevibus papillis minutissimis praeditis differt.

Type: *A. hispanica* Spreng., Syst. Veg. 2, 396 (1826) (= *Stellaria arenaria* L. (1753)).

Syn.: *A. fallax* Bartl. (1912).

A. cerastioides Poir. ssp. *arenarioides* Maire.

A. spathulata sec. Williams (1898) pro parte, non Desf.

K. Sectio Arenaria

Annual plants with multi-nerved sessile leaves, acute to acuminate sepals and petals usually shorter than the sepals; seeds tuberculate, papillose.

Section *Arenaria* is a fairly homogeneous group of annual plants, two of which (*A. serpyllifolia* & *A. leptoclados*) are very widespread throughout Eurasia. The remaining species are more localised, five occurring in the Eastern Mediterranean area. *A. benthamii* in North America and *A. nevadensis* in Spain are however rather isolated from the other species and are only tentatively included in the section; *A. foliacea* shows an approach to Section *Orientales*, while no material has been seen of *A. gorgonea* (Cape Verde Islands) which Williams (1898) related to *A. serpyllifolia*.

In the form of the seedling leaves which rarely persist in the adult plant (persistent in *A. foliacea*), the members of Section *Arenaria* show an affinity with Section *Orientales* and have probably evolved from plants of that type.

K. (i). Series Arenaria

Species: (for full list of synonyms cf. Graebner (1916) under *A. serpyllifolia*, incl. *leptoclados*)

- | | |
|---|--|
| ! <i>A. aegaea</i> Rech. f. (1939) | <i>A. leptoclados</i> Guss. (1845) |
| <i>A. benthamii</i> Torr. & Gray (1840) | <i>A. marschlinii</i> Koch (1841) |
| <i>A. cassia</i> Boiss. (1842) | <i>A. minutiflora</i> Loscos (1876) |
| ! <i>A. conferta</i> Boiss. (1842) | ? <i>A. nevadensis</i> Boiss. (1854) |
| ! <i>A. foliacea</i> Turrill (1954) | ! <i>A. serpentina</i> Jackson (1937) |
| ? <i>A. gorgonea</i> Schmidt (1852) | <i>A. serpyllifolia</i> L. (1753) (type) |
| | ! <i>A. tremula</i> Boiss. (1849) |

K. (ii). Series Saponarioides McNeill, ser. nov.

Plantae xerophyticae: folia et sepala dense glanduloso-pubescentia venis prominentissimis induratis instructa. *Folia* superiora spatulata, venis omnibus similibus praedita. *Inflorescentia* dense conferta; pedicelli brevissimi. *Sepala* ovata. *Capsula* ovoidea vel globosa.

Type: ! *A. saponarioides* Boiss. et Bal. in Boiss., Diagn. Pl. Orient. ser. 2, 6, 35 (1859).

Other species: ! *A. macrosepala* Boiss. (1842).

K. (iii). Series *Cylindricae* McNeill, ser. nov.

A serie *Arenaria* capsula anguste cylindrica (latitudine > 3 -plo longiora) sepala lanceolata (latitudine $3\cdot3\text{--}5$ -plo longiora) anguste acuminata divergit. Planta aliquantum xerophytica: venae sepalorum foliorumque prominentes aliquantum induratae.

Type: *A. guicciardii* Heldr. in Boiss., Diagn. Pl. Orient. ser. 2, 5, 60 (1856).

L. Sectio *Compressae* McNeill, sect. nov.

Sectio in Subgen. *Arenaria* sepalis coriaceo-scariosis seminibus compressis valde distincta.

Herbae perennes ad 45 cm. altae. *Caules* erecti rigidi fragiles; nodi turgidi. *Folia* 10–35 mm. longa late linearia vel lineari-lanceolata, \pm sessilia, nervo mediano praedita; nervus medianus prominens ad medium folium et indistinctus ad apicem percurrrens. *Inflorescentia* c. 8–12-flora, magna diffusa; pedunculi et pedicelli longissimi 10–50 mm. *Sepala* ovata, obtusa (sed in siccis abrupte acuminata, \pm cuspidata, ut videtur), \pm coriacea, late scarioso marginata, vena mediana distincta et venis lateralibus duabus ramulosis obscuris praedita. *Petala* lineari-lanceolata calyce excedentia. *Stamina* fertilia 5 et sterilia (antheris abortis praedita) 5. *Capsula* membranaceo-coriacea valvis vel dentibus longis 6 dehiscens. *Semina* valde compressa, ovato-discoidea (c. $2\cdot5 \times 1\cdot8$ mm.), alata, ad basim (hilum) emarginata, fulva, obscure tuberculata; ala 0·3–0·5 mm. lata, testae productione formata; cotyledones lanceolatae incumbentes canaliculata vel \pm conduplicata, sed radícula exclusa (embryone anti-orthoploco).

Type: *A. compressa* McNeill, nom. nov. (*A. trichotoma* Royle ex Edgew. & Hook. f. in Hook. f., Fl. Brit. Ind. 1, 235 (1874), non Boiss. (1856)).

An extremely distinctive monotypic section from the Western Himalayas and Afghanistan which when more fully known might be better treated at Subgeneric rank.

V. Subgenus *Arenariastrum* Williams in Bull. Herb. Boiss. 3, 599, 602–3 (1895).

Syn.: *Gouffea* Robill. & Cast. ex DC., Fl. Fr. 5 (tom. 6), 609 (1815).

Arenaria d. *Gouffea* (DC.) Fenzl in Endlicher, Gen. Pl. 967 (1840).

Arenaria Sect. *Gouffea* (DC.) Gren. & Godr., Fl. Fr. 1, 262 (1848).

Lectotype: (of *Arenariastrum* = type of *Gouffea*): *A. massiliensis* Fenzl ex Gren. & Godr., Fl. France 1, 262 (1848) (nom. illeg.) = *Gouffea arenarioides* Robill. & Cast. ex DC., l.c. p. 609 (1815) (= *A. gouffea* Chaub.)

Excluded species:

Gouffea crassiuscula Cambess. (1844) = *Lepyrodiclis holosteoides*

Gouffea holosteoides C. A. Meyer (1831) = *Lepyrodiclis holosteoides*

Gouffea stricta (Sibth. & Sm.) Fenzl (1833) = *Buffonia stricta* (S. & S.) Gürke.

The subgenus *Arenariastrum* as established by Williams included three sections, *Gouffea*, *Lepyrodiclis* and *Brachystemma*. Although Williams' description was presumably intended to cover all three groups, in fact

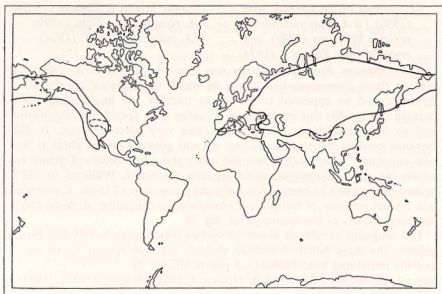


FIG. 3. Geographical distribution of subgenera of *Arenaria*.
 *Arenariastrum* ————— *Eremogone*
 ---- *Eremogoneastrum*

only his Section *Gouffeia* fits it well. ("Sepala . . . rarius subscariosa" suggests that he did not regard *Brachystemma* as typical of the subgenus and he appears to have been unaware that the capsule of *Lepyrodiclis* opens by two valves and is not "4 dentibus . . . dehiscens"). For this reason the type of *Gouffeia* (*G. arenarioides* = *A. gouffeia*) has been selected to typify the subgenus *Arenariastrum*.

The subgenus is confined to a small area in the south of France; it appears to be a bicarpellary derivative of Subgenus *Arenaria* and in habit and sepal structure closely resembles such species as *A. sabulinea* and *A. capillipes*. More detailed studies on the European members of the genus might suggest that it would be better treated merely as another section of the type subgenus (cf. figs. 1 and 3).

Special references: Coste (1901), Rouy & Foucaud (1896).

VI. Subgenus *Eremogoneastrum* Williams in Bull. Herb. Boiss. 3, 598, 601 (1895), pro parte (Sectio i. & Sectio ii. Subsectio 2. p.p.).

Syn.: *Arenaria* Sect. *Eremogoneastrum* (Williams) Pax & Hoffm. in Engler & Harms, Natürl. Pflanzenfam. ed. 2, 16c, 317 (1934).

Lectotype: !*A. festucoides* Benth. in Royle, Ill. Bot. Himal. 81, t.21 f.3 (1839).

Other species:

A. ferruginea Duthie ex Williams (1898)
A. franklinii Dougl. ex Hooker (1833)
A. gulielmi-waldemarii Klotzsch (1862)

A. hookeri Nutt. ex Torrey & Gray (1838)
 !*A. ischnophylla* Williams (1909)
A. kansuensis Maxim. (1889)
 !*A. kumaonensis* Maxim. (1889)
A. monticola Edgew. (1874)

- ! *A. perlevis* (Wms.) Hand.-Mzt. non Triana & Planch. (1862))
 (1930) (\equiv *A. polytrichoides* β *A. pinetorum* A. Nels. (1899)
perlevis Williams (1898) \equiv *A.* ! *A. pulvinata* Edgew. (1874)
musciiformis Edgew. (1874)

The subgenus *Eremogoneastrum* was erected by Williams (1895) to include those *Eremogone*-like plants in which the staminal glands were bifurcate and so appeared to be ten in number. As has already been pointed out (p. 88) this character is no more than specifically diagnostic and so not surprisingly his subgenus was very heterogeneous. It did however contain the nucleus of two natural groups; one of these is the new subgenus *Dolophragma* and the other the scarious-leaved group to which the name *Eremogoneastrum* is now restricted. Williams in 1895 named two species as exemplifying the subgenus; one of these *A. scariosa* is a typical member of Subgenus *Eremogone*, so the other, *A. festucoides* has been chosen as the lectotype (cf. fig. 1).

The subgenus comprises about 10 species which seem to fall into three groups; the three North American species; the type species on its own, and the remaining Sino-Himalayan plants (cf. fig. 3).

Special references: Edgeworth & Hooker (1874), Maguire (1947), (1951).

VII. Subgenus *Eremogone* (Fenzl) Fenzl in Ledebour, Fl. Ross. 1, 360 (1842).

Syn.: *Arenaria* Abteilung "*Orientales*" Spreng., Syst. 2, 401 (1825), nomen invalidum.

Eremogone Fenzl, Versuch Verbreit. Vertheil. Alsin. 13 (1833).

Arenaria a. *Eremogone* (Fenzl) Fenzl in Endlicher, Gen. Pl. 967 (1840)—('Section'—cf. Fenzl l.c., 1842).

Arenaria Sect. *Eremogone* (Fenzl) Edgew. & Hook. f. in Hook. f., Fl. Brit. Ind. 1, 236 (1874), ("*Eremogoneae*").

Arenaria Subgenus *Pentadenaria* Williams in Bull. Herb. Boiss. 3, 598 (1895), pro parte (Sectio *Glomeriflorae* p.p. et Sectio *Rariflorae* Subsectiones 1 and 2).

Arenaria Subgenus *Eremogoneastrum* Williams l.c. 598, pro parte (Sectio ii Subsectio 1.) (excl. spec. typ.).

Arenaria Sect. *Pentadenaria* (Williams) Gürke in Richter & Gürke, Pl. Europ. 2, 275 (1899), pro parte.

Lectotype: *A. graminifolia* Schrad., Hort. Goeth. 1, 5 (1809).

Subgenus *Eremogone* in effect replaces the largely European and Arctic Subgenus *Arenaria* to the East and South, being abundant in Asia and Western North America. Its main centres of diversity are the mountains of Central and South-West Asia and Western North America (cf. fig. 4). It, in its turn, is replaced in China and the Himalayan region by Subgenera *Eremogoneastrum* and *Dolophragma*.

Special references: Fenzl in Ledebour (1842), Maguire (1947), (1951), Schischkin & Knorring in Komarov (1936).

Key to Sections and Series

- 1a. Capsule 1-seeded, ovary with 2 ovules; stamens 5 alternating with inner whorl of 5 staminodes; sepals narrowly lanceolate, long acuminate; cotyledons accumbent (C. Asia) B. Sect. *Monogone*
 1b. Capsule many-seeded; stamens 10 2

- 2a. Leaves long linear or setaceous, not spiny, the leaves of the vegetative rosettes erect tufted (2-)2.5-25 cm. long; (when < 4 cm., sepals often \pm entirely herbaceous, not strongly indurate); sepals various but always with a median herbaceous or coriaceous-herbaceous portion running \pm to the apex; plants erect or tufted or with \pm creeping caudiculi, never forming cushions; cotyledons always accumbent 3
- 2b. Leaves short (0.5-1.5 (-2) cm.), setaceous rather spiny, or if rather longer (to 3 cm.) \pm pungent; leaves of the vegetative rosettes closely crowded together all appressed or the outer spreading, rarely all erect (& plants \pm tufted) and then sepals subcoriaceous or almost entirely scarious; sepals usually strongly indurate at the base; plants forming spiny cushions, occasionally suffruticose and sometimes loosely-tufted 6
- 3a. Sepals always obtuse, the median portion \pm herbaceous with (1-)3 or more parallel nerves, the margins coriaceous to scarious; cauline leaves linear, grass-like, 5-25 cm. long, 1-2.5 mm. broad; inflorescence many-flowered (E. Europe and S.W. Asia)

C. Sect. *Eremogone*

- 3b. Sepals acute, acuminate or cuspidate, often becoming obtuse when flattened (the thin membranous margin being normally recurved), rarely truly obtuse and then obscurely nerved and cauline leaves often short 4-8 cm. long, subsetaceous, 0.5-1 mm. broad 4
- 4a. Sepals at and after anthesis appearing cuspidate by the inrolling of the thin membranous margin at the apex, obscurely nerved, the median coriaceous-herbaceous portion dark brown, purple or black, at least at the tip (forming the cusp); basal part of the sepals often coriaceous in flower; receptacle and basal part of the calyx ligneous in fruit; cauline leaves linear grass-like (S.W. Asia)

D. Sect. *Glomeriflorae*

- 4b. Sepals acute or acuminate or appearing so, sometimes obtuse, never cuspidate 5
- 5a. Sepals mostly coriaceous to scarious with a broad scarious margin, ovate to lanceolate, narrowly acute to long acuminate (sometimes obtuse when flattened), buff, or midrib green, never darkened; plants caudiculate loosely tufted; rosette leaves (5-)8-20 cm. long (E. Europe and S.W. Asia) E. (i). Sect. *Rigidae* Series *Rigidae*
- 5b. Sepals almost entirely herbaceous with a narrow membranous margin, broadly ovate, obtuse, or else linear-lanceolate, narrowly acute to acuminate, tip often darkened; plants densely tufted from a thick caudex; rosette leaves short 4-8(-12) cm. long. (Panarctic, W. North America, C. Asia, Caucasus) A. Sect. *Capillares*

- 6a. Leaves with one very prominent nerve and 2-4 fine laterals, or 3(-5) \pm equally prominent, pungent or spiny setaceous; sepals not strongly indurate, linear-lanceolate, long acuminate, \pm flat, with a median nerve and many (4-6) parallel lateral nerves; inflorescence few-flowered; petals shorter than or \pm equal to sepals; capsule coriaceous; cotyledons incumbent (Spain and N. Africa)

H. Sect. *Pungentes*

- 6b. Leaves one-nerved or obscurely nerved, setaceous, spiny (or rarely pungent and then sepals ovate, obtuse); sepals usually strongly indurate at the base, convex or keeled, obscurely nerved or with a single median nerve, or flat and multinerved and then ovate, obtuse; inflorescence few-many-flowered; capsule usually ligneous; cotyledons accumbent 7
- 7a. Sepals subglabrous, obscurely nerved, not or scarcely carinate, the central coriaceous (or herbaceous) portion merging with the broad scarious margins and apex, apex bluntly acute, obtuse or almost fimbriate; flowers aggregated into dense clusters or if inflorescence lax, sepals almost entirely scarious; petals shorter or a little longer than sepals; plants sometimes tufted and rosette leaves erect (E. Turkey & Iran) F. Sect. *Scariosae* 8
- 7b. Sepals distinctly nerved (unless densely pubescent), the herbaceous portion running to the apex and \pm clearly demarcated from the (usually narrow) membranous or rarely scarious margin; inflorescence usually lax, or if congested sepals narrowly acuminate, sometimes flowers solitary; petals always much longer than sepals; plants pulvinate or suffrutescent, outer rosette leaves spreading or all very short appressed 9
- 8a. Staminal glands five, indistinct, at the base of the outer whorl of stamens; sepals with a distinct \pm parallel-sided coriaceous-herbaceous median strip, very gradually narrowing to the tip
F. (i). Series *Polycnemifoliae*
- 8b. Staminal glands deeply bifurcate (arms 0.3-0.5 mm. long), appearing as ten alternating with the stamens; sepals with a \pm triangular coriaceous-herbaceous portion merging into the scarious margin and never extending right to the tip . . . F. (ii). Series *Scariosae*
- 9a. Sepals 5-8 mm. long, lanceolate, with a broad scarious margin, only the prominent keel herbaceous; inflorescence 1(-3)-flowered; plant densely caespitose; leaves setaceous, not or scarcely spiny, those of the sterile rosettes \pm appressed. (Turkish Kurdistan)
E. Sect. *Rigidae* (ii). Series *Setaceae*
- 9b. Sepals 2-6 mm. long, broadly ovate to lanceolate with a rather narrow membranous or subscarious margin; inflorescence many-flowered, rarely 1-few-flowered and then sepals ovate or obscurely nerved; plant usually either suffruticose or forming spiny cushions, the outer sterile rosette leaves often spreading or the fascicles dense small and axillary, occasionally leaves appressed, not spiny, and then sepals short (< 5 mm.) and obscurely nerved (not at all keeled) (S.W. Asia: Afghanistan-Turkey, W. North America)
G. Sect. *Sclerophyllae*

A. Sectio Capillares McNeill, sect. nov.

Syn.: ?*Brewerina* A. Gray in Proc. Amer. Acad. 8, 620 (1872).

Arenaria Subgenus *Eremogone* Series *Sclerophyllae* sec. Schischkin in Komarov, Fl. U.R.S.S. 6, 529 (1936), pro parte, non Boiss.

Plantae dense caespitosae; turiones steriles et caules floriferi \pm dense conferti. *Folia* turionum sterilium erecta, setacea, (2-)2.5-10 cm. longa, 0.5-1 mm. lata. *Inflorescentia* 6-25 cm. alta, \pm pauciflora (3-7). *Sepala*

linear-lanceolata vel ovata, obtusa vel acuta vel longe (raro abrupte) acuminata, subherbacea saepe leviter indurata. *Petala* calyce longiora. *Capsula* sublignosa calycem vix excedens, dentibus longis 6 dehiscens. Type: *A. capillaris* Poir., *Encycl. Meth.* 6, 380 (1804).

Other species:

- | | |
|---|---|
| <i>A. acicularis</i> Williams (1909) | <i>A. formosa</i> Fisch. ex Ser. (1824) |
| <i>A. congesta</i> Nutt. ex Torr. & Gray (1838) | <i>A. juncea</i> M. Bieb. (1819) |
| <i>A. eastwoodii</i> Rydb. (1904) | (!) <i>A. lychnidea</i> M. Bieb. (1808) |
| <i>A. fendleri</i> A. Gray (1849) | <i>A. meyeri</i> Fenzl (1842) |
| | ? <i>A. mongolica</i> Schischk. (1937) |

Section *Capillares* with its holarctic distribution is possibly the most primitive group of *Eremogone*; the relationship with Section *Sclerophyllae*, is particularly close and it is sometimes difficult to draw the dividing line. In Asia species such as *A. formosa* come very near to Section *Sclerophyllae* while in North America, at least one of Maguire's (1946, 1947) varieties of *A. congesta* (var. *charlestonensis*—possibly also var. *crassula*) is typical of Section *Sclerophyllae*. The variety in question would seem, however, better attached to the sclerophyllous *A. kingii* in which congestion of the inflorescence also occurs. The geographically isolated Caucasian *A. lychnidea* is distinctive among Eurasian plants in its very weakly developed staminal glands and in its sepal structure shows an approach to Section *Glomeriflorae*. In North America, in the Colorado—New Mexico region, there are two species (*A. eastwoodii* and *A. fendleri*) with very narrow pointed sepals; this characteristic is also found in a Tibetan species (*A. acicularis*), and makes these species readily distinguishable from the rest of the section. Full synonymy of the North American species is to be found in Maguire (1947 and 1951).

B. Sectio *Monogone* Maxim. in *Bull. Acad. Sci. St.-Petersb.* 26, 436 (1880).

Syn.: *Arenaria* Subgenus *Monogone* (Maxim.) Schischkin in Komarov, *Fl. U.R.S.S.* 6, 536 (1936).

Type: ! *A. potaninii* Schischk. l.c. (1936) (= *A. pentandra* Maxim. (1880), non Dufour (1820)).

A monotypic group endemic to the Tien Shan and Altai regions. In general facies and in leaf and sepal structure it is typical of Subgenus *Eremogone* and the reduced androecium and gynoecium do not seem to warrant separation at more than sectional rank. The plant appears related to Section *Capillares* of which it is probably a reduced derivative; it differs also in the rather spiny leaves (as in Section *Sclerophyllae*) and in the narrower long acuminate sepals reminiscent of Section *Rigidae* (cf. fig. 4).

C. Sectio *Eremogone*

Syn.: *Arenaria* Subgenus *Eremogone* Divisio "*Rariflorae*" Subdivisio "*Xerolemmae*" Fenzl in Ledebour, *Fl. Ross.* 1, 361 (1842), (nomen invalidum).

Arenaria Series *Xerolemmae* Fenzl ex Schischkin in Komarov, *Fl. U.R.S.S.* 6, 525 (1936).

Species (and species names):

- | | |
|--|--|
| <i>A. asiatica</i> Schischk. (1930) | ! <i>A. blepharophylla</i> Boiss. (1867) |
| <i>A. biebersteinii</i> Schlecht. (1816) | (incl. ! <i>A. steveniana</i> Boiss. (1867)) |

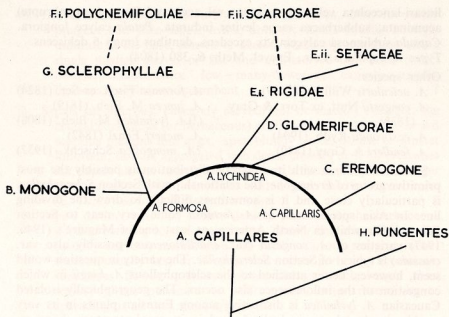


FIG. 4. Diagram of the probable inter-relationships and evolution of the sections and series of *Arenaria* subgenus *Eremogone*.

- | | |
|---|--|
| <i>A. filifolia</i> M. Bieb. (1808), non Forsk. | <i>A. oosepala</i> Bordz. (1931) |
| (!) <i>A. graminea</i> C. A. Mey. (1831) | <i>A. pineticola</i> Klokov (1952) |
| <i>A. graminifolia</i> Schrad. (1809) (type) | <i>A. polaris</i> Schischk. (1936) |
| <i>A. isaurica</i> Boiss. (1867) | ? <i>A. saxatilis</i> L. (1753) |
| <i>A. koriniana</i> Fisch. ex Fenzl (1842) | <i>A. stenophylla</i> Ledeb. (1823) (ex Klokov, 1952?) |
| <i>A. longifolia</i> M. Bieb. (1808) | <i>A. syreistochikowii</i> Smirnov (1939) |
| <i>A. micradenia</i> Smirnov (1939) | <i>A. ucranica</i> Spreng. ex Klokov (1952) |

Section *Eremogone* is distributed from Central and Eastern Europe across to Central Asia and extends south into the Caucasus, Armenia and probably S. Turkey. The type species, *A. graminifolia*, is very polymorphic and Smirnov (1939) and Klokov (1947, 1952) have divided it into a large number of microspecies.

D. Sectio *Glomeriflorae* Fenzl ex Williams in Bull. Herb. Boiss. 3, 602 (1895) (sub Subgen. *Pentadenaria*).

Syn.: *Arenaria* Subgenus *Eremogone* Divisio "*Rariflorae*" Subdivisio "*Chromolemmae*" Fenzl in Ledebour. Fl. Ross. 1, 365 (1842) (nomen invalidum).

Arenaria Subgenus *Eremogone* Series *Glomeriflorae* (Fenzl ex Williams) Schischkin in Komarov, Fl. U.R.S.S. 6, 520 (1936).

Arenaria Subgenus *Eremogone* Series *Chromolemmae* Fenzl ex Schischkin l.c. p. 528 (1936).

Type: *A. dianthoides* J. E. Smith, Icon. ined. 16, t.16 (1789).

Other species:

A. cucubaloides Sm. (1789)

A. gypsophiloides L. (1767)

The section is confined to the Caucasus, E. Turkey and Iran and appears to have evolved from the basic *Capillares* stock by way of plants similar to *A. lychnidea* (cf. fig. 4).

E. Sectio *Rigidae* McNeill, sect. nov.

Syn.: *Arenaria* Subgenus *Eremogone* Series "*Rigidae*" Schischkin in Komarov, Fl. U.R.S.S. 6, 521 (1936) (descr. rossice).

Plantae caespitosae. *Folia* setacea vel linearia. *Inflorescentia* cymosa pauci- vel multi-flora, laxa vel saepe congesta; bracteae latissime scarioso-marginatae. *Sepala* ovata vel lanceolata, anguste acuta vel acuminata, late scarioso-marginata.

Section *Rigidae* resembles Section *Eremogone* in having its main centre of distribution in E. Europe, S. Russia and the Caucasus. It does not, however, extend into Central Asia, but occurs in Eastern Turkey and N.W. Iran. The section is closely related to Section *Capillares* with which it was linked by Fenzl in Ledebour (1842) (both in his "*Chromolemmae*") and from which it has probably evolved by the sepals becoming more hardened, coriaceous, scarious, and acuminate. In the Series *Setaceae* it shows some affinity with Sections *Sclerophyllae* and *Scariosae* (cf. fig. 4).

E. (i). Series *Rigidae*

Plantae laxae caespitosae, erectae, 15–50 cm. altae. *Folia* turionum sterilius subsetacea vel linearia (graminea), 5–20 cm. longa; folia caulina graminea. *Inflorescentia* cymosa multiflora, laxa vel congesta. *Sepala* maxime coriaceo-scariosa, late scarioso-marginata. *Petala* sepalis breviora vel subaequilonga. *Capsula* calyce inclusa, lignea.

Type: *A. rigida* M. Bieb., Fl. Taur.-cauc. 1, 346 (1808).

Other species:

A. cephalotes M. Bieb. (1808)

(!) *A. holostea* M. Bieb. (1808)

! *A. szowitsii* Boiss. (1867)

E. (ii). Series *Setaceae* McNeill, ser. nov.

Plantae dense caespitosae vel subpulvinatae. *Folia* omnia brevina (0.5–1.5 cm. longa), setacea. *Inflorescentia* c. 5 mm. alta, 1(–3)-flora. *Sepala* lanceolata, latissime scariosa, subcarinata; pars herbacea (carina) anguste oblonga. *Petala* sepalis multo longiora.

Type: ! *A. angustisepala* McNeill in Notes Roy. Bot. Gard. Edinb. 23, 510 (1961).

F. Sectio *Scariosae* McNeill, sect. nov.

Plantae caespitosae (plerumque dense) vel spinoso pulvinatae, caudices et caudiculi crassi praeditae. *Folia* rigida spinosa vel setacea 5–20 mm. longa; folia rosularum sterilius erecta vel \pm patentia. *Inflorescentia* \pm pauciflora (2–10) plerumque congesta. *Sepala* ex toto coriaceo-herbacea vel scariosa, obscure nervosa sed interdum subcarinata. *Petala* calyce breviora vel sublongiora.

Type: ! *A. scariosa* Boiss., in Tchihatch, Asie Min. Bot. 1, 234 (1860).

A highly evolved section of five species in Northern Iran and Turkish Armenia, but absent from the Caucasus; its affinities appear to lie on the one hand with Section *Rigidae* Series *Rigidae* which it resembles in sepal

structure, and on the other with Section *Sclerophyllae* with which it shares the sclerophyllous habit (cf. fig. 4).

F. (i). Series *Polycnemifoliae* McNeill, ser. nov.

Flores in inflorescentiis partialibus densis terminalibus vel axillaribus semper aggregati. *Sepala* aliquantum anguste scarioso-marginata; pars coriaceo-herbacea \pm anguste oblonga, mediana, ad apicem percurrentes. *Glandulae staminorum* 5 indivisae ad basim staminorum exteriorum positae.

Type: *A. polycnemifolia* Boiss., Diagn. Pl. Orient. ser. 1, 1, 48 (1842).

Other species:

A. pseudacantholimon Bornm. (1910) *A. zargariana* Parsa (1947)

F. (ii). Series *Scariosae*

Sepala scariosissima; pars coriaceo-herbacea basalis sub-triangularis in apicem et marginem scariosum transiens. *Petala* calyce semper sublongiora. *Glandulae staminorum* exteriorum bipartitae ut 10 inter stamina positae videantur.

Species:

A. armeniaca Boiss. (1842) *A. scariosa* Boiss. (1860) (type).

G. Sectio *Sclerophyllae* (Boiss.) McNeill, stat. nov.

Syn.: *Arenaria* §2 *Sclerophyllae* Boiss., Fl. Orient. 1, 690 (1867).

Arenaria Series *Sclerophyllae* (Boiss.) Schischkin in Komarov, Fl. U.R.S.S. 6, 529 (1936).

Lectotype: *A. ledebouriana* Fenzl, Illustr. Fl. Syr. Taur. 45 (1843) (reprint from Russegger, Reise, 1 (2), 931).

Other species:

<i>A. aberrans</i> M. E. Jones (1930)	<i>A. litwinowii</i> Schischk. (1932)
<i>A. acerosa</i> Boiss. (1849)	<i>A. macradenia</i> S. Wats. (1882)
<i>A. aculeata</i> S. Wats. (1871)	? <i>A. mongolica</i> Schischk. (1937)
! <i>A. acutisepala</i> Hausskn. ex Williams (1898)	<i>A. multiflora</i> Gilli (1956)
<i>A. calcicola</i> Gilli (1956)	<i>A. paulsenii</i> Winkl. (1901)
! <i>A. davisii</i> McNeill (1961)	! <i>A. persica</i> Boiss. (1842)
! <i>A. drypidea</i> Boiss. (1842)	<i>A. pumicola</i> Coville & Leiberg (1897)
? <i>A. ferganica</i> Schischk. (1932)	<i>A. stenomeres</i> Eastwood (1944)
<i>A. griffithii</i> Boiss. (1853)	! <i>A. tetrasticha</i> Boiss. (1842)
! <i>A. insignis</i> Litw. (1907)	<i>A. tschuktschorum</i> Regel (1862)
<i>A. kingii</i> (S. Wats.) M. E. Jones (1896)	<i>A. ursina</i> Robins. (1894)

Section *Sclerophyllae* is probably a xerophytic derivative of the holarctic Section *Capillares* and as such occurs in two disjunct areas, the steppes of Central and South-West Asia and the dry regions of the Western United States. In both areas the species have been very confused taxonomically, and like Section *Capillares* but unlike most other groups of Subgenus *Eremogone*, its members seem to be in a state of active evolution and speciation (cf. fig. 4).

Despite its apparent polyphyletic origin, no satisfactory discrimination can be made between the Asian and North American species of the Section. Within each, however, there is considerable variation; in North America the very pungent leaved *A. stenomeres* holds an isolated position and is very different from the pungent Iranian species, *A. persica* (= *A. lessertiana*)

and *A. insignis*, while the small and not very spiny-leaved *A. tetrasticha* and *A. davisii* (S. Iran and E. Turkey) could perhaps form a third group to be separated from the main aggregation of rather spiny caespitose or suffruticose species.

H. Sectio *Pungentes* McNeill, sect. nov.

Plantae pulvinatae vel dense caespitosae, spinosae. *Folia* rigida setacea vel pungentia, 3–30 mm. longa, nervo mediano prominentissimo et nervis lateralibus 2–4 (saltem ad basim) vel nervis 3(–5) aequalibus praedita. *Inflorescentia* 1–3-flora. *Sepala* lineari-lanceolata vel ovato-lanceolata, longe acuminata, leviter indurata, nervo mediano prominenti et nervis lateralibus parallelis 4–6 praedita. *Petala* calyce breviora vel subaequilonga. *Capsula* subcoriacea, nec lignea, calyce inclusa. *Semina* (vix matura) spadicea aspera; cotyledones incumbentes.

Type: *A. pungens* Clem. in Lagasca, Gen. Sp. Nov. 15 (1816).

Other species: *A. mairei* Emberger (1933).

Section *Pungentes*, confined to Spain and North Africa, is a very isolated group whose nearest affinities are not apparent. The type species has usually been placed in *Eremogone* and because of its semi-terete pungent leaves and superficial resemblance to *A. stenomeris* and *A. persica*, it is retained for the present in that subgenus; it differs however from the members of the other sections in that its cotyledons are incumbent and not accumbent. It is even more distant from Subgenus *Arenaria* (in which the cotyledons are always incumbent) and with more evidence may come to be placed in a subgenus of its own.

VIII. Subgenus *Dolophragma* (Fenzl) McNeill, comb. et stat. nov.

Syn.: *Dolophragma* Fenzl in Ann. Wien. Mus. 1, 63, t.71 (1836).

Cherleria sec. D. Don, Prodr. Fl. Nepal. 214 (1825), non L. (1753).

Lectotype: !*A. globiflora* (Fenzl) Edgew. in Hook. f., Fl. Brit. Ind. 1, 238 (1874).

Other species:

! <i>A. densissima</i> Edgew. (1874)	! <i>A. przewalskii</i> Maxim. (1880)
! <i>A. lichiangensis</i> W. W. Smith (1913)	! <i>A. smithiana</i> Mattf. (1932)
! <i>A. oreophila</i> Hooker (1874)	(≡ <i>A. oresbia</i> W. W. Smith
! <i>A. polytrichoides</i> Edgew. (1874)	(1920), non Greenm. (1904))
s.s.	

Considerable confusion exists in the identification and classification of the densely pulvinate Sino-Himalayan *Arenarias*. Much of this is due to the failure to distinguish between those plants with long pointed sepals and scarious leaf margins to which the name *Eremogoneastrum* is now confined and those with short obtuse sepals and a swollen coriaceous leaf margin. This latter group includes the two species on which Fenzl founded his genus *Dolophragma* (in the false belief that the capsule was partially septate) and that name is adopted for the new subgenus. The species included within the group show a gradation from very densely pulvinate types such as *A. polytrichoides* (sensu stricto), *A. densissima* and *A. globiflora* to linear-leaved densely caespitose species like *A. smithiana* and *A. przewalskii*. The subgenus is probably made up of seven species, all in the Sino-Himalaya region.

IX. Subgenus **Solitaria** McNeill, **nom. nov.**

Syn.: *Arenaria* Subgenus *Euarenaria* Sect. *Sikkimenses* Williams in Bull. Herb. Boiss. 3, 600 (1895).

Lectotype: *A. ciliolata* Edgew. in Hook. f., Fl. Brit. Ind. 1, 240 (1874).

Other species:

- | | |
|--|--|
| ! <i>A. forrestii</i> Diels (1912) | ! <i>A. roseotincta</i> W. W. Smith (1913) |
| ! <i>A. glanduligera</i> Edgew. (1874) | |
| ! <i>A. ramellata</i> Williams (1909) | <i>A. stracheyi</i> Edgew. (1874) |

Williams distinguished his section *Sikkimenses* within the type subgenus principally on the basis of its solitary flowers, and thereby included within it a number of very dwarf alpine species with a reduced inflorescence, whose true affinities lie elsewhere. As here defined it forms a small but very distinctive group with solitary flowers, broad leaves, and the sepals hardened (coriaceous) at the apex and margins. *A. glanduligera* is rather atypical in that the sepals lack this coriaceous tip and possibly shows an approach to Subgenus *Odontostemma* (e.g. *A. monantha* Williams). There are probably five species in the group; *A. forrestii* Diels being apparently conspecific with the earlier *A. ramellata* Williams. The new substantive name *Solitaria* has been chosen to accord with the form of name in the other Subgenera of *Arenaria* and *Minuartia*.

Special reference: Edgeworth & Hooker (1874).

X. Subgenus **Odontostemma** (G. Don) Williams in Bull. Herb. Boiss. 3, 603 (1895).

Syn.: *Odontostemma* Benth. ex G. Don, Gen. Syst. 1, 449 (1831) ("Adenostemma" Hook. f.).

Arenaria Sect. *Macrogynae* Franchet in Bull. Soc. Bot. Fr. 33, 432 (1886).

Arenaria Sect. *Odontostemma* (G. Don) Pax in Engler & Prantl, Natürl. Pflanzenfam. 3 (1b), 84 (May 1889); Franchet, Pl. Delavay., 93 (1889).

Arenaria Sect. *Moehringella* Franchet, Pl. Delavay, 96 (1889).

Arenaria Subgenus *Odontostemma* Sectiones *Barbatae* & *Yunnanenses* (= *Odontostemma*) Williams l.c. 603 (1895).

Arenaria Subgenus *Macrogynae* (Franchet) Williams l.c. 603 (1895).

Goeringia Williams in Bull. Herb. Boiss. 5, 530 (1897).

Moehringella (Franchet) Neumayer in Verh. Zool-Bot. Ges. Wien, 78, p. (14) (1924).

Type: *A. blinkworthii* McNeill, **nom. nov.**: *Odontostemma glandulosum* Benth. ex G. Don, Gen. Syst. 1, 449 (1831) = *A. glandulosa* (G. Don) Williams (1895), non Jacq. (1798), = *A. benthamii* Edgew. in Hook. f. (1874), non Fenzl ex Torrey & Gray (1840).

Other species:

- | | |
|---|--|
| ! <i>A. barbata</i> Franchet (1886) | <i>A. giraldui</i> (Diels) Mattf. (1932) |
| ! <i>A. cerastiformis</i> Williams (1909) | ! <i>A. inconspicua</i> Hand.-Mzt. (1929) |
| ! <i>A. debilis</i> Hooker (1874) | ! <i>A. inornata</i> W. W. Smith (1920) |
| ! <i>A. delavayi</i> Franchet (1886) | ! <i>A. ionandra</i> Diels (1912) |
| <i>A. dsharaensis</i> Pax & Hoffm. (1922) | ! <i>A. leucasteria</i> Mattf. (1932) |
| ! <i>A. euodonta</i> W. W. Smith (1920) | <i>A. linearifolia</i> Franchet (1889), non Poir. (1804) |
| <i>A. fridericae</i> Hand.-Mzt. (1920) | |

- | | |
|--|---|
| !A. <i>littledalei</i> Hemsley (1896) | A. <i>reducta</i> Hand.-Mzt. (1920) |
| A. <i>longistyla</i> Franchet (1886) | A. <i>roseiflora</i> Sprague (1916) |
| A. <i>melanandra</i> (Maxim.) Mattf. ex
Hand.-Mzt. (1929) | A. <i>saginoidea</i> Maxim. (1880) |
| !A. <i>melandryiformis</i> Williams (1909) | !A. <i>salweenensis</i> W. W. Smith
(1920) |
| !A. <i>melandryoides</i> Edgew. (1874) | !A. <i>schneideriana</i> Hand.-Mzt.
(1920) |
| ?!A. <i>monantha</i> Williams (1909) | !A. <i>szechuensis</i> Williams (1899) |
| !A. <i>napuligera</i> Franchet (1886) | !A. <i>thangoensis</i> W. W. Smith
(1911) |
| !A. <i>nigricans</i> Hand.-Mzt. (1929) | A. <i>trichophora</i> Franchet (1886) |
| !A. <i>pogonantha</i> W. W. Smith
(1920) | !A. <i>weissiana</i> Hand.-Mzt. (1920) |
| ?A. <i>quadridentata</i> (Maxim.)
Wms. (1898) | !A. <i>xerophila</i> W. W. Smith (1920) |
| | !A. <i>yunnanensis</i> Franchet (1886) |

Subgenus *Odontostemma* is a natural group of about thirty species in the eastern Himalayas and the mountains of South-Western China. In habit it is relatively unspecialised and in this it parallels the predominantly South American subgenus *Leiosperma* (Fig. 1) and the type subgenus centred in Europe; it differs from both however in its floral structure particularly in the reduction to two carpels.

As here circumscribed, *Odontostemma* includes the genera *Gooringia* and *Moehringella*, neither of which as originally defined, warrant taxonomic recognition at any rank (cf. pp. 96-97).

It was also found impossible to maintain as distinct from *Odontostemma* Franchet's Section *Macrogyne* (Subgenus in Williams), supposedly differing in the length of the style. Further study however will undoubtedly reveal subdivisions of *Odontostemma*, and *Macrogyne* and possibly even *Moehringella* and *Gooringia* may come to typify sections or series within the group.

Special references: Franchet (1886), (1889), Handel-Mazzetti (1929), Mattfeld (1932), Neumayer (1924), Smith (1913), (1919), (1920), Williams (1909a).

2. *Moehringia* L.

Moehringia L., Sp. Pl. 359 (1753) et Gen. Pl. ed. 5, 170 (1754); Pax & Hoffmann in Engler & Harms, Natürl. Pflanzenfam. ed. 2, 16c, 319 (1934).

Syn.: *Arenaria* Subgenus vel Sectio *Moehringia* (L.) Benth. in Benth. & Hook. f., Gen. Pl. 1, 150 (1862).

Strophium Dulac, Fl. Hautes-Pyr. 247 (1867) (= *Moehringia*).

Arenaria Section *Moehringia* (L.) Post & Kuntze, Lexicon 43 (cf. Preface p. V.) (1903).

Type: *M. muscosa* L., Sp. Pl. 359 (1753).

Key to Sections

- 1a. Leaves not narrowly linear, subulate, or semi-terete, the lower usually elliptical to ovate, the upper linear-lanceolate to ovate, flowers pentamerous (very rarely tetramerous—forms of *M. papulosa*)

The new Section *Pseudomoehringia*, confined to Spain and North Africa, is most markedly distinguished by its *Arenaria*-like seeds. A strophiole is of course present (unlike *Arenaria*) but it is possible that this is not homologous with that found in the other members of the genus (cf. key). This raises the question as to whether the genus *Moehringia* may not be diphyletic, or perhaps that the species of Section *Pseudomoehringia* might be more correctly placed within *Arenaria* itself (cf. Discussion of seed characters, p. 92, and generic evaluation, p. 95).

The other three sections form a more homogeneous group and it is rather difficult to draw dividing lines between them. This is particularly so in the case of the Sections *Diversifoliae* and *Moehringia*. *M. villosa* (*Diversifoliae*) is supposed to have elliptical lower leaves but these are frequently absent in fruiting specimens and the species is obviously very close to *M. pendula*, which Nyman and Graebner place in Section *Moehringia* (\equiv *Augustifoliae*). It has been thought better to confine the latter section to those species, many of which are tetramerous with narrow linear (or semi-terete) leaves; *M. pendula* and *M. papulosa* have therefore been transferred to Section *Diversifoliae*. (*M. grisebachii* to which Graebner refers under *Diversifoliae*, has entirely linear leaves and is therefore placed in Section *Moehringia*).

Special references: Bornmüller (1919), Graebner in Ascherson & Graebner (1915-16) pp. 449-469, Nyman (1876) p. 112, Pax & Hoffmann (1934) (bibliography), Schischkin in Komarov (1936) pp. 540-544.

A. Sectio *Pseudomoehringia* McNeill, sect. nov.

Herbae perennes, caespitosae vel tegetiformes, 5-20 cm. altae, caudiculis fragilibus numerosis praeditae. *Folia* suborbiculata vel oblanceolata, latissime acuta, in petiolum brevem sensim attenuata. *Inflorescentia* terminalis 2-5-flora; pedicelli longi (10-40 mm.); bractae minutae, subulato-setaceae. *Sepala* ovata, acuta, obscure nervata. *Petala* oblanceolata vel obovata, longe attenuata, sepalis multo longiora. *Semina* reniformia obscure reticulata; strophiolium fuscum, evidentere tuberculis longis dense compactis formatum.

Type: !*M. intricata* Willk., Enum. Pl. Nov. Rar. Hisp. Austr. 14 (1852). Other species:

- | | |
|---|--------------------------------|
| ? <i>M. alleizettei</i> Battand. (1917) | <i>M. fontqueri</i> Pau (1930) |
| ! <i>M. tejedensis</i> Willk. (1893) | |

B. Sectio *Latifoliae* Nyman ex Graebner in Ascherson & Graebner, Syn. Mitt.-Eur. Fl. 5 (1), 449 (1915).

Lectotype: *M. trinervia* (L.) Clairv., Man. Herb. 150 (1811).

Other species: (cf. also synonymy given by Graebner, 1915-16).

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|--|---|
| <i>M. elongata</i> Schischk. (1936) | ! <i>M. platysperma</i> Maxim. (1873) |
| <i>M. lateriflora</i> (L.) Fenzl (1833) | <i>M. radiolata</i> Pančič (1874) |
| <i>M. macrophylla</i> (Hook.) Fenzl (1833) | ! <i>M. stellarioides</i> Cosson (1862) |
| <i>M. minutiflora</i> Bornm. (1919) | <i>M. umbrosa</i> (Bunge) Fenzl (1833) |
| ! <i>M. pentandra</i> J. Gay (1832) | |

C. Sectio *Diversifoliae* Nyman ex Graebner in Ascherson & Graebner, Syn. Mitt.-Eur. Fl. 5 (1), 453 (1915), sensu ampl.

Lectotype: *M. diversifolia* Dolliner ex Koch in Flora 22, 2 (1839).

Other species:

- | | |
|--|--|
| ! <i>M. jankae</i> Griseb. ex Janka (1873) | <i>M. pendula</i> (W. & K.) Fenzl (1833) |
| <i>M. papulosa</i> Bertol. (1839) | <i>M. villosa</i> (Wulf.) Fenzl (1833) |

D. Sectio *Moehringia*

Syn.: *M. Sect. Angustifoliae* Nyman ex Graebner in Ascherson & Graebner, Syn. Mitt.-Eur. Fl. 5 (1), 455 (1915).

Species:

- | | |
|--|--|
| <i>M. bavarica</i> (L.) Gren. (1841) | <i>M. glaucovirens</i> Bertol. (1844) |
| " <i>M. bornmuelleri</i> Anger." (cf. Hayek, Öst. Bot. Zeit. 52, 149 (1902)). | ! <i>M. grisebachii</i> Janka (1873) |
| <i>M. ciliata</i> (Scop.) Dalla Torre (1882) (= <i>M. polygonoides</i> (Wulf.) Mert. & Koch (1831)). | <i>M. insubrica</i> Degen (1926) |
| <i>M. dasyphylla</i> Bruno (1804) | ! <i>M. malyi</i> Hayek (1902) |
| <i>M. dielsiana</i> Mattf. (1925) | ! <i>M. markgraffii</i> Merxmüller & Guterma (1957) |
| <i>M. frutescens</i> Panizzi (1889) | <i>M. muscosa</i> L. (1753) (type) |
| | <i>M. sphagnoides</i> (Froel. ex Reichb.) Bluff, Nees & Schauer (1837) |
| | <i>M. tommasinii</i> Marches. (1880) |

Excluded species:

- M. linearifolia* (Franch.) Williams = *Arenaria linearifolia*.
M. nemorosa (Kunth) Fenzl ex Hemsley = *Arenaria nemorosa*.
M. nodosa (L.) Clairv. = *Sagina nodosa* (L.) Fenzl.
M. sedoides (L.) Clairv. = *Minuartia sedoides* (L.) Hiern (Sect. *Spectabiles* Subsect. *Cherleria*).
M. stricta Sibth. & Sm. = *Buffonia stricta* (Sibth. & Sm.) Gütke.
M. subulata Clairv. = *Sagina saginoides* (L.) Karst.
M. thomasiana J. Gay = *Minuartia grigneensis* (Reichb.) Mattf. (Sect. *Lanceolatae* Series *Grigneenses*).

3. *Brachystemma* D. Don

Brachystemma D. Don, Prodr. Fl. Nepal. 216 (1825); Benth. in Benth. & Hook. f., Gen. Pl. 1, 149 (1862); Pax & Hoffmann in Engler & Harms, Natürl. Pflanzenfam. ed. 2, 16c, 319 (1934).

Syn.: *Arenaria* Subgenus *Arenariastrum* Section *Brachystemma* (D. Don) Williams in Bull. Herb. Boiss. 3, 603 (1895).

Type: *B. calycinum* D. Don, Prodr. Fl. Nepal. 216 (1825) (= *A. nepalensis* Spreng., non *A. calycina* Poir.)

Other species: ? *B. ovatifolium* Mizushima (1955).

A genus of one or two species, the type species common in the Himalayas and southern China and extending into Siam and Indo-China. A second species was recently described from Tibet, but no material has been seen and on the basis of the description there must remain some doubt as to its correct taxonomic position (cf. fig. 5).

4. *Honkenya* Ehrh.

Honkenya Ehrhart, Beitr. Naturk. 2, 180 (1788) ("*Honckenia*" Rafin., "*Stonckenya*" Rafin., "*Honckenya*" Bartl., "*Honkeneja*" Endl., "*Honckeneya*" Steud., "*Honckeneja*" Maxim.); non *Honckenya* Willd. (1793)–

Tiliaceae; Pax & Hoffmann in Engler & Harms., *Naturl. Pflanzenfam.* ed. 2, **16c**, 328 (1934).

Syn.: "*Ammodenia*" J. G. Gmelin ex S. G. Gmelin, *Fl. Sibir.* **4**, 160 (1769), pro syn. *Arenariae peploides*.

Ammonalia Desv. in *J. Bot. Desv. ser. 2*, **3** (5), 223 (1816) (\equiv *Honkenya*).

Halianthus Fries, *Fl. Halland.* 75 (1817).

Adenarium Rafin., *New Fl. N. Amer.* **1**, 62 (1836).

Arenaria b. *Halianthus* (Fries) Reichb. in Mössler, *Handb. Gewächsk.* ed. 2, **1**, 740 (1827) ("Section"—Pfeiffer, *Nomenclator* (1870)).

Ammodenia J. G. Gmelin ex Rupr., *Beitr. Pfl. Russ.* **2**, 25 (1845) ("*Ammadenia*").

Arenaria Subgenus vel Sectio *Ammodenia* (Rupr.) Benth. in Benth. & Hook. f., *Gen. Pl.* **1**, 151 (1862).

"*Hallia*" Dumort. ex Pfeiffer, *Nom.* **1**, 1549 (1874), in syn.

Alsine Sect. *Honkenya* (Ehrh.) Pax in Engler & Prantl., *Naturl. Pflanzenfam.* **3** (1b), 83 (1889).

Minuartia Sect. *Honkenya* (Ehrh.) Mattf. in *Bot. Jahrb.* **57** Beibl. no. **126**, 27 (1921).

Type: *H. peploides* (L.) Ehrh., *Beitr.* **2**, 181 (1788).

A genus of a single polymorphic species complex.

Special references: Fernald (1909), Graebner (1918) pp. 695–698, Mattfeld (1922) pp. 8–12, Pobedimova (1960), Williams (1909).

5. *Wilhelmsia* Reichb.

Wilhelmsia Reichb., *Consp.* 206 (1828), non Koch (1848).

Syn.: *Merckia* Fisch. ex Cham. & Schlecht. in *Linnaea* **1**, 59 (1826) ("*Merkia*" Reichb.), non *Merckia* Borkh. (1792); Pax & Hoffmann in Engler & Harms., *Naturl. Pflanzenfam.* ed. 2, **16c**, 333 (1934).

Arenaria Subgenus vel Sectio *Merckia* (Cham. & Schlecht.) Benth. in Bentham & Hook. f., *Gen. Pl.* **1**, 151 (1862).

Arenaria Sect. *Merckia* (Cham. & Schlecht.) Post & Kuntze, *Lexicon* 43 (cf. Preface p. V.) (1903).

Species:

W. physodes (Ser.) McNeill (1960).

Excluded species:

Merckia peploides (L.) G. Don \equiv *Honkenya peploides*.

A monotypic genus confined to Arctic regions of eastern Asia and North-western America (cf. fig. 5).

Special references: Hultén (1928) p. 88, McNeill (1960), Maguire (1951).

6. *Minuartia* L.

Minuartia L., *Sp. Pl.* 89 (1753) et *Gen. Pl.* ed. 5, 100 (1754); Pax & Hoffmann in Engler & Harms., *Natürl. Pflanzenfam.* ed. 2, **16c**, 329 (1934).

Syn.: *Alsine* sec. Crantz, *Inst.* **2**, 404 (1766); Gaertn., *De Fruct.* **2**, 223 (1791) et auctt. saeculi XIX, non L., *Sp. Pl.* 272 (1753), nec auctt. plur. amer. anni 1890–1925.

Arenaria L. Subgenus vel Sectio *Alsine* Benth. in Benth. & Hook. f., Gen. Pl. 1, 150 (1862), quoad descr. et syn. nec quoad basionom.

Alsinopsis Small, Fl. S.-E. U.S. 419 (1903).

Cherleria L. sensu ampl. Sampaio, Lista Herb. Portug. 82 (1913).

Type species: *M. dichotoma* L. (cf. Hitchcock in Hitchcock & Green (1929); Stearn (1957) pp. 136-142).

The genus *Minuartia* as a whole comprises 115 to 130 species, distributed throughout the Northern Hemisphere and with one species native in Chile.

Evolution from mesophytic perennial types has proceeded in two main directions; towards xerophytic perennial groups such as Section *Sclerophyllae* and some species of Sections *Lanceolatae* and *Acutiflorae*, and towards annual groups such as Section *Sabulina* chiefly in the Old World and Sections *Uninerviae* and *Greniera* in the New. Mattfeld's interpretation of these annual groups as being primitive cannot be accepted, and the present order of Sections and Series consequently represents considerable change from his arrangement.

Key to Subgenera

- 1a. Stamens and petals subperigynous arising on or at the top of a very short calyx tube, inner whorl of stamens frequently adnate to the petals; leaves ovate to linear, rounded or bluntly obtuse at the apex; petals frequently pink; cotyledons accumbent; plants perennial (Mediterranean, Atlantic Is., E. Africa) I *Rhodalsine*
- 1b. Stamens and petals arising from a hypogynous disc, petals & stamens always free to the base; leaves frequently linear-subulate, if broader then acute to acuminate. II *Spergella*
- 2a. Cotyledons accumbent; seeds pyriform with a dorsal groove, obscurely tuberculate, papillose on the dorsal surface; petals pink, rarely white, emarginate; plants annual; leaves setaceous, single-nerved, usually subtending axillary fascicles of equally long leaves (the leaves superficially appearing to be whorled) (S.W. Asia)
- 2b. Cotyledons incumbent; seeds usually reniform (discoïd in Sect. *Greniera*) with a flat or rounded dorsal ridge; petals white, rarely pink (*M. labillardierei*—Sect. *Spectabiles*, a caespitose to pulvinate perennial); fascicular leaves when present, shorter than the subtending cauline leaves III *Hymenella*
- 3a. Sepals and capsule valves spreading in fruit; stems \pm quadrangular; seeds reniform, verrucose (Mexico) IV *Minuartia*
- 3b. Sepals (and capsule valves) erect in fruit; stems terete or subterete

I. Subgenus *Rhodalsine* (J. Gay) Graebner in Ascherson & Graebner, Syn. Mitt.-Eur. Fl. 5 (1), 774 (1918).

Syn.: *Alsine* 13 *Psammophilae* Fenzl in Endlicher, Gen. Pl. 965 (1840).
 "Psammante" Reichb., Repert. Herb. Nomencl. 205 (1841), nomen.

Alsine n. *Psammophilae* (Fenzl) Endlicher, Enchir. 505 (1843) ("Psammophila").

Rhodalsine J. Gay in Ann. Sci. Nat. ser. 3, 4, 25 (1845).

Arenaria Subgenus vel Sectio *Rhodalsine* (J. Gay) Benth. in Benth. & Hook. f., Gen. Pl. 1, 150 (1862).

Alsine § 1. *Rhodalsine* (J. Gay) Boiss., Fl. Orient. 1, 669 (1867).

Alsine Sect. *Rhodalsine* (J. Gay) Amo y Mora, Fl. Espana Port. (Herb. Penins. Iber.) 6, 133 (1873).

Alsine Subgenus *Rhodalsine* (J. Gay) Pax in Engler & Prantl, Natürl. Pflanzenfam. 3 (1b), 83 (1889).

Minuartia Sect. *Psammophilae* (Fenzl) Mattf. in Bot. Jahrb. 57 Beibl. No. 126, 33 (1921).

Type: *M. procumbens* (Vahl) Graebner l.c. (1918).

Other species and synonyms (cf. also Williams (1898a) for names in *Arenaria*).

<i>Alsine gayana</i> Webb ex Christ (1888), non <i>R. geniculata</i> var. <i>gayana</i> Williams, nec <i>M. gayana</i> (Wms.) Maire	<i>M. geniculata</i> (Poir.) Thellung (1912) <i>M. platyphylla</i> (Christ) McNeill* <i>M. vestita</i> (Baker) McNeill†
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Plants of Subgenus *Rhodalsine* are common throughout the more southerly Mediterranean coasts extending to Portugal and the Canary Islands and with a distinctive species in Somaliland. Throughout the greater part of its range, however, the subgenus is only represented by one rather variable species for which *M. geniculata* is the correct name. (Williams, 1898a, recognised two species in this area but the criteria by which he distinguished the other, *M. procumbens*, are not at all satisfactory—cf. also Jackson, 1933). On the Canary Islands one or possibly two other distinct taxa occur; one of these (*Alsine gayana* Christ) may not be specifically separable from *M. geniculata*, but the other, which Maire in 1936 called *M. gayana* but which was first published (in 1888 with the same type) as *Alsine platyphylla* certainly seems to merit specific recognition. The third distinct species is the Somaliland plant which Baker described as *Arenaria vestita* and whose true position has not previously been noted.

Special references: Christ (1888), Jackson (1933), Williams (1898a).

II. Subgenus *Spergella* (Fenzl) McNeill, stat. nov.

Syn.: *Alsine* 10. *Spergella* Fenzl in Endlicher, Gen. Pl. 965 (1840), non *Spergella* Reichb.

"*Phlebanthia*" Reichb., Repert. Herb. Nomencl. 205 (1841), nomen.

Alsine Sect. *Spergella* (Fenzl) Fenzl in Ledeb., Fl. Ross. 1, 356 (1842).

Minuartia Sect. *Spergella* (Fenzl) Mattf. in Bot. Jahrb. 57 Beibl. No. 126, 33 (1921).

Type: *M. picta* (Sibth. & Sm.) Bornm. in Beih. Bot. Zbl. 28 (2), 148 (1911).

* *M. platyphylla* (Gay ex Christ) McNeill, comb. nov.

Syn.: (≡) *Alsine platyphylla* Gay ex Christ, Spicil. Canar. in Bot. Jahrb. 9, 159 (1888).

(≡) *Rhodalsine geniculata* var. *gayana* Williams in Bull. Herb. Boiss. 6, 10 (1898) ("δ")

(≡) *M. gayana* (Wms.) Maire in Bull. Soc. Hist.-Nat. Afr. Nord. 27, 213 (1936), in obs.

† *M. vestita* (Baker) McNeill, comb. nov.

Syn.: *Arenaria vestita* Baker in Kew Bull. 1895 p. 212 (1895).

Other species: *M. formosa* (Fenzl) Mattf. (1921).

A very distinctive group of two sympatric species in the Irano-Turanian to Saharo-Sindian regions of the Levant, southern Turkey and Iraq.

III. Subgenus *Hymenella* (Moç. & Sessé ex Ser.) McNeill, stat. nov.

Syn.: *Hymenella* Moç. & Sessé ex Ser. in DC., Prodr. 1, 389 (1824).

Triplateia Bartl. in Presl, Rel. Hankeanae 2, 11 (1831).

Arenaria Subgenus vel Sectio *Hymenella* (Ser.) Benth. in Benth. & Hook. f., Gen. Pl. 1, 150 (1862).

Alsine Sect. *Hymenella* (Ser.) Rohrb. in Linnaea 37, 246 (1872).

Minuartia Sect. *Hymenella* (Ser.) Mattf. in Bot. Jahrb. 57 Beibl. No. 126, 27 (1921).

Type: *M. moehringioides* (Moç. & Sessé ex Ser.) Mattf. in Bot. Jahrb. 57 Beibl. No. 126, 27 (1921).

The distinctive facies of the single species of this subgenus makes its retention within *Minuartia* open to question but in the absence of any more definite characters than the quadrangular stem and the spreading calyx and capsule, it has been thought wisest to follow Mattfeld's treatment, but raising it to subgeneric rank. *M. moehringioides* is only known from Central Mexico.

IV. Subgenus *Minuartia*

Key to Sections, Subsections and Series

(modified from Mattfeld 1922)*

- 1a. Seeds strongly compressed, discoid, winged by the expansion of the testa; staminal glands prominent, simple or with a broad hyaline flap (c. 0.6 mm. diam.) on the outside, surrounding the introrse nectar pit, the stamen borne on the middle of the interior face of the gland; plants annual; petals entire (W. North America) K. Sect. *Greniera*
- 1b. Seeds \pm reniform, occasionally fimbriate or crested, never winged; glands indistinct or prominent, simple, globular or quadrate, and the stamen \pm terminal, or bifurcate and the stamen lying between the two arms 2
- 2a. Annual or biennial herbs; petals \pm emarginate, twice as long as the calyx; sepals obscurely or reticulately nerved, erect at anthesis; leaves 1-nerved (or almost 3-nerved), slender or rather fleshy; seeds obscurely tuberculate to tuberculate, sometimes echinate (W. North America) J. Sect. *Uninerviae*
- 2b. Suffrutescent or herbaceous perennials, or if annuals petals shorter than or \pm equal to calyx; petals entire very rarely shortly emarginate (never in annual species) 3
- 3a. Sepals rounded to obtuse at apex, linear; calyx cylindrical (Holarctic & Temperate) A. Sect. *Spectabiles* 4
- 3b. Sepals acute or acuminate, rarely obtuse and then ovate; calyx ovoid or urceolate 8

* Many of Mattfeld's names were originally published (Mattfeld 1921) as *nomina nuda*: only the references to the place of valid publication are given in the enumeration that follows this key.

- 4a. Petals longer than calyx, usually very prominent; sepals erect at anthesis; staminal glands subglobose or minutely emarginate; leaves flat or subterete 5
- 4b. Petals filiform shorter than the calyx or often absent; sepals spreading at anthesis; staminal glands deeply bipartite; leaves triquetrous; sterile shoots gradually passing into flowering shoots (C. Europe, Scotland) A. b. Subsect. *Cherleria*
- 5a. Flowering shoots very distinct, not producing turions or bearing fascicles of leaves (rarely with small ones); leaves slender or rigid, obscurely or 3-5-nerved A. c. Subsect. *Laricifoliae* 6
- 5b. Sterile shoots gradually passing into flowering shoots, rarely flowering shoots distinct and then bearing large fascicles; leaves fleshy, rarely rather rigid, traversed by 1 \pm prominent nerve A. a. Subsect. *Spectabiles* 7
- 6a. Leaves densely imbricate toward the apex of the sterile shoot forming a small rosette, 3-5-nerved, flat and linear-lanceolate or linear-setaceous and sometimes becoming \pm triquetrous towards the apex (Caucasus, Armenia etc.) A. c. (i). Series *Caucasicae*
- 6b. Leaves of sterile shoots \pm fasciculate, never rosulate-spreading, linear-subulate or setaceous \pm semiterete, obscurely nerved or \pm 1-3-nerved at the base; petals rarely pink (C. & S. Europe, Levant) A. c. (ii). Series *Laricifoliae*
- 7a. Leaves flat, lanceolate or linear-lanceolate; entire leaf, or the margin near the base, setose, bearing long acute hairs; seeds with a fimbriate crest on the dorsal ridge (W. Arctic, N. America, Arctic & E. Asia & Caucasus) A. a. (i). Series *Laricinae*
- 7b. Leaves linear-subulate, the margin near the base \pm scabrid with short obtuse hairs, rarely glabrous; seeds obscurely reticulate to obscurely tuberculate all over (Pan Arctic, W. North America, C. Asia, N. Europe & Alps) A. a. (ii). Series *Spectabiles*
- 8a. Leaves recurved, rigid with a very thick median nerve; fascicular leaves spreading; seeds irregularly rugulose to obscurely tuberculate (N. America) E. Sect. *Sclerophyllae* (& 3 Series)
- 8b. Leaves of the sterile rosettes closely fasciculate, or if spreading, slender 9
- 9a. Petals shorter than sepals; sepals erect at anthesis; leaves 1-nerved; seeds obscurely tuberculate; perennial herbs with elongate pedicels (Holarctic, C. Asia & C. Europe) H. Sect. *Alsinanthe*
- 9b. Petals longer than sepals, or if shorter sepals spreading at anthesis 10
- 10a. Plants annual, sepals 1-3-nerved, or perennial and sepals usually 1-nerved (rarely 3); calyx often hardened at the base (always so in perennial plants); seeds obscurely tuberculate, papillose or echinate 11
- 10b. Plants perennial; sepals 3-many (5-9)-nerved with a rather narrow membranous or scarious margin; calyx not hardened at the base 18
- 11a. Calyx not or scarcely hardened at the base; sepals 3-nerved; seeds small (0.25-0.7 mm. long. diam.), plants always annual M. Sect. *Sabulina* 12

- 11b. Calyx strongly hardened at the base; sepals 3-nerved, or 1-nerved with a broad white coriaceous margin; seeds large (0.7-1.5 mm. long diam.) (C. & S. Europe, N. & E. Africa, S.W. Asia) L. Sect. *Minuartia* 13
- 12a. Petals white with translucent dots; leaves single-nerved, fleshy, spathulate; very slender annuals (Chile, California) M. (ii). Series *Californicae*
- 12b. Petals entirely white; leaves usually 3-nerved, subulate, rarely spathulate; slender or often robust annuals (Europe, W. Asia, N. Africa, W. North America) M. (i). Series *Sabulina*
- 13a. Sepals 3-nerved (outer sometimes 5-nerved) with a very narrow white margin, the central green portion extending beyond the lateral nerves; plants annual L. a. Subsect. *Minuartia* 14
- 13b. Sepals 1-nerved, nerve white with two narrow green lines on either side and with broad white scarious margins (rarely 3-nerved and then green portion not extending beyond the lateral nerves & plant perennial); plants usually perennial, sometimes biennial or annual (often overwintering) L. b. Subsect. *Xeralsine* 15
- 14a. Leaves linear to linear-lanceolate, flat, 5-7(-9)-nerved, the basal margin glabrous, scabrid or sparsely clothed with erect glandular hairs; bracts similar to the leaves, shorter or longer than the partial inflorescences; seeds few-many, dark brown, obscurely tuberculate (E. & W. Mediterranean) L. a. (i). Series *Montanae*
- 14b. Leaves setaceous, narrowing from the base, basal margin lanuginose with long crisp hairs; bracts elongate, recurved or incurved, longer than the partial inflorescences; seeds few (1-4) yellow-brown, opaque, obscurely reticulate or \pm smooth (E. & W. Mediterranean) L. a. (ii). Series *Minuartia*
- 15a. Sepals prominently 3-nerved; flowers aggregated into terminal clusters; plants perennial (Southern Turkey) L. b. (i). Series *Leucocephalae*
- 15b. Sepals 1-nerved (or with 2 weak lateral nerves at the base and then flowers not clustered) 16
- 16a. Plants annual; partial inflorescences sessile, glomerulate; sepal nerves with prominent crystals*; calyx infundibular; seeds few; stems and upper leaf bases clothed with crisped glandular hairs (Spain & N. Africa) L. b. (iv). Series *Campestres*
- 16b. Plants perennial, biennial, or rarely annual; inflorescence lax, or partial inflorescences densely fasciculate, usually pedunculate; sepal nerves without prominent crystals; calyx often truncate; seeds usually many 17
- 17a. Plants biennial, rarely annual or perennial; inflorescences densely fasciculate, clothed with long straight spreading hairs (C. & S. Europe) L. b. (iii). Series *Xeralsine*
- 17b. Plants perennial, often suffruticose; inflorescence laxly dichasial to densely corymbose or subcapitate; indumentum various (often glabrous, puberulent or with erect hairs, rarely lanuginose or with spreading hairs) (C. & E. Europe, N. Africa, S. W. Asia) L. b. (ii). Series *Setaceae*

* Appearing as disc-like swellings, visible with a hand lens.

- 18a. Sepals 5-7(-9)-nerved, rarely 3-nerved and then seeds fimbriate 19
 18b. Sepals 3-nerved; seeds obscurely tuberculate and sometimes
 echinate 24
- 19a. Leaves linear-subulate or setaceous; sepals spreading at anthesis;
 seeds obscurely tuberculate or muricate (Mountains of C. & S.E.
 Europe, S.W. Asia) B. Sect. *Plurinerviae*
- 19b. Leaves lanceolate or linear-lanceolate, rarely linear; sepals erect or
 scarcely spreading at anthesis; seeds fimbriate on the dorsal
 ridge 20
- 20a. Flowers pentamerous (Mountains of C. & S. Europe & S.W. Asia)
 C. Sect. *Lanceolatae* 21
- 20b. Flowers tetramerous (Alps) D. Sect. *Aretioideae*
- 21a. Leaves narrowly linear; sepals 3-nerved; glabrous herbs; pedicels
 elongate much longer than the calyx; sepals ovate, acute spreading
 at anthesis; capsule a little longer than calyx; petals lanceolate,
 contracted at the base into a claw (Alps)
 C. (iv). Series *Grigneenses*
- 21b. Leaves lanceolate, obovate, oblong, linear-lanceolate or narrowly
 triangular, never narrowly linear; sepals 5-many nerved;
 peduncles and pedicels glandular pubescent; pedicels very short,
 scarcely exceeding calyx 22
- 22a. Sepals many-nerved or if only 5-nerved, marginal nerves conspicuous
 beyond the middle, acuminate; inflorescence few-flowered (rarely
 1); capsule shorter than calyx 23
- 22b. Sepals 5-nerved, marginal nerves inconspicuous and evanescent
 above the middle, acute, suberect to sub-spreading at anthesis;
 inflorescence 1 (rarely 2)-flowered; capsule much longer than
 calyx; petals ovate contracted into a claw (C. Europe)
 C. (iii). Series *Lanceolatae*
- 23a. Petals longer than or rarely equalling sepals, obovate, narrowly
 cuneate at the base; stems terete, short, 0.5-5(-7) cm. tall; bracts
 similar to all the stem leaves (mainly C. & S. Europe)
 C. (i). Series *Graminifoliae*
- 23b. Petals shorter than the sepals ovate to lanceolate abruptly contracted
 at the base, clawed or sessile; stems angled, elongate, 4-20 cm.
 tall; bracts broader than at least the lower cauline leaves (S. W.
 Asia) C. (ii). Series *Dianthifoliae*
- 24a. Sepals acuminate, erect at anthesis; petals obovate or oblong
 gradually narrowing to the base, 1.5-2 times as long as sepals
 (C. & S. Europe, W. & C. Asia) F. Sect. *Acutiflorae* 25
- 24b. Sepals acute spreading at anthesis; petals ovate abruptly con-
 tracted at the base into a claw, about as long as or a little longer
 than sepals (N. Temperate & Subarctic regions & mountains S.
 to 35°-40° N.) G. Sect. *Tryphane*
- 25a. Leaves of sterile shoots spreading at anthesis (usually widely so),
 rather long (12-20 mm.), herbaceous flat and linear-lanceolate to
 hard \pm terete, never subulate-setaceous (rarely leaves short,
 3-10 mm., and then linear-lanceolate and rather fleshy); the

median nerve of the leaves thicker than the laterals or leaves one-nerved (Spain, C. Europe, W. & C. Asia to Kashmir & Pakistan)

F. (i). Series *Acutiflorae*

25b. Leaves of sterile shoots densely fasciculate to somewhat spreading, short, 4–10 mm. long, subulate-setaceous, rarely linear . . . 26

26a. Leaves of sterile shoots usually somewhat spreading with three \pm equal nerves, narrowly linear to subulate-setaceous; petals oblanceolate (Greece & S. Turkey) . . . F. (ii). Series *Pichleriae*

26b. Leaves of sterile shoots densely fasciculate, one-nerved or with lateral nerves present only at the base, subulate-setaceous to semi-terete; petals obovate (Asia Minor)

F. (iii). Series *Umbelluliferae*

A. Sectio *Spectabiles* (Fenzl) Hayek, Fl. Steierm. 1, 274 (1908).

Syn.: *Alsine* 7 *Spectabiles* Fenzl in Endlicher, Gen. Pl. 965 (1840).

Wierzbickia Reichb. [Repert. Herb. Nomencl. 205 (1841)–nomen], Ic. Fl. Germ. 5, 30 (1841).

Alsine Sect. *Spectabiles* (Fenzl) Fenzl in Ledebour, Fl. Ross. 1, 352 (1842).

Lectotype: *M. biflora* (L.) Schinz & Thell. in Bull. Herb. Boiss. ser. 2, 7, 403 (1907).

Section *Spectabiles* probably contains the least highly evolved forms of Subgenus *Minuartia*; one species, *M. rhodocalyx*, has generally five carpels, which may represent a primitive character. The section as a whole comprises about twenty species distributed on the mountains of Eurasia and throughout the Arctic.

A. a. Subsectio *Spectabiles*

A. a. (i) Series *Laricinae* Mattf.* in Fedde Rep. Beih. 15, 182 (1922).

Lectotype: *M. laricina* (L.) Mattf. in Bot. Jahrb. 57 Beibl. No. 126, 33 (1921).

Other species:

M. brotherana (Trautv.) Woronow . . . *M. macrocarpa* (Pursh) Ostenf.
(1914) . . . (1920)

M. colchica Kharadze (1938) . . . *M. rhodocalyx* (Alb.) Woronow

M. imbricata (M.B.) Woronow . . . (1914)

M. inamoena (C. A. Mey.) Woronow . . . *M. trautvetteriana* Sosnowsky &
(1914) . . . Kharadze (1938)

A series of two species widely distributed in Western North America and Arctic Asia, extending south to Japan, and of a species complex in the Caucasus, considered by Kharadze (1938) to comprise six species.

A. a. (ii). Series *Spectabiles*

Syn.: *Minuartia* Sect. *Spectabiles* Series *Biflorae* Mattf. in Fedde Rep. Beih. 15, 182 (1922) – diagn. in clave.

Species:

M. arctica (Steven) Graebn. (1918) . . . *M. obtusiloba* (Rydb.) House

M. biflora (L.) Schinz & Thell. . . (1921) (? incl. *M. marcescens*
(1907) (type) . . . (Fern.) House (1921))

* Mattfeld (1921, 1922) consistently uses the symbols §1, §2, etc. to indicate the rank below "Section"; this has been equated with "Series" on the basis of his reference to §4. *Campestres* as "ser. nov." (Mattfeld 1922 p. 54).

A series of three species throughout Arctic Eurasia and extending southwards into western United States and central Asia (to the Himalayas).

A. b. Subsectio *Cherleria* (L.) McNeill, stat. nov.

Syn.: *Cherleria* L., Sp. Pl. 425 (1753) et Gen. Pl. ed. 5 194 (1754).

Alsine 8 *Cherleria* (L.) Fenzl in Endlicher, Gen. Pl. 965 (1840) ("*Cherleriae*").

Alsine Sect. *Cherleria* (L.) Fenzl in Ledeb., Fl. Ross. 1, 356 (1842) ("*Cherleriae*").

Arenaria Subgenus vel Sectio *Cherleria* (L.) Benth. in Benth. & Hook. f., Gen. Pl. 1, 150 (1862).

Arenaria Sect. *Cherleria* (L.) Post & Kuntze, Lexicon 42 (1903) (cf. Preface p. V.) ("*Cherlera*").

Alsine Subgenus *Cherleria* (L.) C. E. Moss, Cambr. Br. Fl. 3, 32, 36 (1920).

Minuartia Sect. *Cherleria* (L.) Mattf. in Fedde Rep. Beih. 15, 211 (1922).

Type: *M. sedoides* (L.) Hiern in J. Bot. Lond. 37, 320 (1899).

Excluded species:

"*C. bipartita*" Fisch. ex Steud. = ?
(1841)

C. bisulca Bartl. (1830) ≡ *Arenaria bisulca* (Bartl.) Rohrb.
(Subgenus *Dicranilla*)

C. dichotoma (L.) Sampaio (1913) ≡ *Minuartia dichotoma* L. (Section
& Series *Minuartia*)

C. dicranoides Cham. (1826) ≡ *Arenaria chamissonis* Maguire
(Subgenus *Arenaria* ?Sect. *Rariflorae*)

C. geniculata (Poir.) Sampaio (1913) ≡ *Minuartia geniculata* (Poir.)
Thellung (Subgenus *Rhodalsine*)

C. grandiflora D. Don (1825) = *Arenaria globiflora* (Fenzl) Edgew.
(Subgenus *Dolophragma*)

C. imbricata Ser. (1824) = *Minuartia cherlerioides* (Hoppe)
Becherer (Sect. *Aretioideae*)

C. juniperina D. Don (1825) ≡ *Arenaria densissima* Edgew. (Sub-
genus *Dolophragma*)

C. laevis Bartl. (1825) = ?

C. nitida Bartl. (1825) ≡ *Arenaria nitida* (Bartl.) Rohrb.
Subgenus *Leiosperma* or *Dicranilla*)

C. octandra Sieber ex Spreng. (1825) = *Minuartia cherlerioides* (Hoppe)
Becherer (Sect. *Aretioideae*)

"*C. peduncularis*" Bunge ex Steud. = ?
(1841) ("= *C. bipartita*")

C. sedoides sec. Forsk. (1775) = *Minuartia geniculata* (Poir.)
Thellung (Subgenus *Rhodalsine*)

C. sedoides sec. Sibth. & Sm. (1806) = *Minuartia confusa* (Boiss.) Maire
& Petitm. (Section *Minuartia*
Series *Xeralsine*)

C. sedoides sec. Turcz. (1842) = *Stellaria* sp. (fide Index Kewensis)

- C. sibirica* Regel & Tiling (1859) = *Minuartia biflora* (L.) Schinz & Thell. (Sect. & Series *Spectabiles*)
C. stellata Clarke (1816) = *Minuartia stellata* (Clarke) Maire & Petitm. (Sect. *Lanceolatae* Series *Graminifoliae*)
C. tenuifolia (L.) Sampaio (1913) = *Ar. tenuifolia* L. = *Minuartia hybrida* (Vill.) Schischk. (Sect. & Series *Sabulina*)
C. verna (L.) Sampaio (1913) = *Minuartia verna* (L.) Hiern (Sect. *Tryphane*)

A monotypic group restricted to the mountains of Central Europe and the Scottish Highlands.

A. c. Subsectio *Laricifoliae* (Mattf.) McNeill, stat. nov.

Syn.: *Minuartia* Sect. *Spectabiles* Series *Laricifoliae* Mattf. in Fedde Rep. Beih. **15**, 182 (1922).

Lectotype: *M. laricifolia* (L.) Schinz & Thell. in Bull. Herb. Boiss. ser. 2, **7**, 403 (1907).

A. c. (i). Series *Caucasicae* Mattf. in Fedde Rep. Beih. **15, 182 (1922).**

Lectotype: *M. caucasica* (Adams ex Rupr.) Mattf. in Ascherson & Graebner, Syn. Mitt.-Eur. Fl. **5** (1), 941 (1919), nom. illeg. = *M. circassica* (Albow) Woronow (1914).

Other species: *M. aizoides* (Boiss.) Bornm. (1914).

A series of two species in Western Anatolia and the Caucasus.

A. c. (ii). Series *Laricifoliae*

Syn.: *Minuartia* Sect. *Spectabiles* Series *Laricifoliae* Mattf. et Series *Labillardiereae* Mattf. in Fedde Rep. Beih. **15**, 182 (1922).

Species:

- | | |
|---|--|
| <i>M. baldaccii</i> (Halácsy) Mattf. (1919) | <i>M. labillardierei</i> Briquet (1911) |
| <i>M. capillacea</i> (All.) Graebn. (1918) | <i>M. laricifolia</i> (L.) Schinz & Thell. (1907) (type) |
| <i>M. garckeana</i> (Boiss.) Mattf. (1922) | <i>M. wettsteinii</i> Dörfel. ex Mattf. (1922) |
| <i>M. handelii</i> Mattf. (1923) | |

A series of seven species on the mountains of Southern Europe extending into N.W. Anatolia and in the Lebanon mountains (one species).

B. Sectio *Plurinerviae* McNeill, nom. nov.: *Minuartia* Sect. *Tryphane* sec. Mattf. in Fedde Rep. Beih. **15, 113 (1922) (descr.), non Fenzl emend. Boiss. (1867).**

Syn.: *Alsine* 3 *Tryphane* Fenzl in Endlicher, Gen. Pl. 965 (1840), pro parte excl. lectotyp.

Tryphane (Fenzl) Reichb., Repert. Herb. Nomencl. 205 (1841), pro parte excl. lectotyp.

Type: *M. recurva* (All.) Schinz & Thell. in Bull. Herb. Boiss. ser. 2, **7**, 404 (1907).

Other species:

- | | |
|--|--|
| <i>M. bulgarica</i> (Velen.) Graebn. (1918) | <i>M. hirsuta</i> (M.B.) Hand.-Mzt. (1909) |
| <i>M. engleri</i> Mattf. (1922) | |
| <i>M. eurytanica</i> (Boiss. & Heldr.) Hand.-Mzt. (1909) | <i>M. juressi</i> (Schlecht.) Lacaita (1930) |

A section comprising about six closely related species on the mountains of Central and Southern Europe and S.W. Asia.

Fenzl named two "species prototyp." for his infrageneric group *Tryphane*—*Alsine recurva* and *A. verna*. When he divided the group into two Sections Mattfeld chose *recurva* as lectotype, ignoring the fact that Boissier, more than 50 years before, had by excluding that species (and placing it in the *Lanceolatae*) effectively typified *Tryphane* by *Alsine verna*. A new name is, therefore, required for this very homogeneous section which includes *M. recurva* and *M. hirsuta*; the name *Plurinerviae*, which has been given (above), refers to the 5–7-nerved sepals, the major distinguishing feature between this section and *Tryphane* s.s. (= *Polymechana* Mattf.).

C. Sectio *Lanceolatae* (Fenzl) Graebner in Ascherson & Graebner, Syn. Mitt.-Eur. Fl. 5 (1), 756 (1918).

Syn.: *Alsine* 5 *Lanceolatae* Fenzl in Endlicher, Gen. Pl. 965 (1840).

Alsine Sect. *Lanceolatae* (Fenzl) Fenzl in Ledebour, Fl. Ross. 1, 350 (1842).

Type: *M. lanceolata* (All.) Mattf. in Bot. Jahrb. 57 Beibl. No. 126, 31 (1921) = *M. rupestris* (Scop.) Schinz & Thell.

C. (i). Series *Graminifoliae* Mattf. in Fedde Rep. Beih. 15, 130 (1922), diagn. in clave.

Syn.: *Petteria* Reichb. [Repert. Herb. Nomencl. 205 (1841) – nomen] Ic. Fl. Germ. 5, 33 (1841).

Lectotype: *M. graminifolia* (Arduino) Javorka in Fl. Hung. exs. Cent. 2, 142 Schedae 22 (1914).

Other species:

M. saxifraga (Friv.) Graebner *M. stellata* (Clarke) Maire & Petitm. (1908)

A series of three species in South-Eastern Europe (centred in the Balkans) extending into N.W. Anatolia (*M. saxifraga* subsp. *tmolea*).

C. (ii). Series *Dianthifoliae* Mattf. in Fedde Rep. Beih. 15, 130 (1922)–diagn. in clave.

Lectotype: *M. dianthifolia* (Boiss.) Hand.-Mzt. in Ann. Naturh. Hofmus. Wien, 26, 147 (1912).

Other species:

M. acuminata Turrill (1929) *M. pestalozzae* (Boiss.) Bornm. (1915)

A series of three species with a restricted distribution in Asia Minor, Nakhichevan & Northern Iran.

C. (iii). Series *Lanceolatae*

Syn.: *Dufourea* Grenier in Act. Soc. Linn. Bord. 9, 25 (1837) pro parte, non Bory ex Willd. (1810), nec Kunth (1818).

Facchinia Reichb. [Repert. Herb. Nomencl. 204 (July 1841)–nomen], Ic. Fl. Germ. 5, 29 (1841).

Alsine e. *Dufourea* (Gren.) Endlicher, Enchir. Bot. 505 (1843).

Alsine Sect. *Facchinia* (Reichb.) Griseb., Spicil. Fl. Rumel. 1, 202 (Dec. 1843–Jan. 1844).

Minuartia Sect. *Lanceolatae* Series *Lanceolatae* (Fenzl) Mattf. in Bot. Jahrb. 57 Beibl. No. 126, 31 (1921).

Minuartia Sect. *Lanceolatae* Series *Cerastiifoliae* Mattf. in Fedde Rep. Beih. **15**, 136 (1922).

Species:

M. cerastiifolia (Ram. ex DC.) *M. rupestris* (Scop.) Schinz & Graebn. (1918) Thell. (1907) (incl. *M. lanceolata*—type)

A series of two species, one confined to the Alps, the other to the Pyrenees.

C. (iv). Series *Grigneenses* Mattf. in Fedde Rep. Beih. **15**, 130 (1922)—“*Grigneenses*”.

Type: *M. grigneensis* (Reichb.) Mattf. l.c. (1921) (“*M. grigneensis* (Thomas)”).

A monotypic series endemic to the Bergamo Alps in Northern Lombardy.

The species was first named “*Arenaria grigneensis*” by Thomas in 1842 without a description. Reichenbach, when he validated the name (in *Tryphane*) a few months later (1842–43), used the spelling “*grigneensis*”. As it is named after the Grigna mountain group, this seems a deliberately chosen spelling, and being in the first valid publication of the name, must be regarded as the correct form. Mattfeld uses “*grigneensis*” and consequently his series was originally spelled “*Grigneenses*”; this is amended to accord with the correct spelling of the specific epithet.

D. Sectio *Aretioideae* (Fenzl) Mattf. in Fedde Rep. Beih. **15**, 144 (1922).

Syn.: *Siebera* Schrad. ex Hoppe in Flora **2**, 24 (1819), non J. Gay (1827) nom. cons.

Someraueria Hoppe l.c. 26 (1819).

Cherleria a. *Someraueria* (Hoppe) Reichb., Consp. 206 (1828).

Alsine 4. *Aretioideae* Fenzl in Endlicher, Gen. Pl. 965 (1840).

Alsine d. *Someraueria* (Hoppe) Endlicher, Enchir. Bot. 505 (1841) (“*Sommeraueria*”).

Alsine Sect. *Aretioideae* (Fenzl) Fenzl in Ledeb., Fl. Ross. **1**, 350 (1842).

Alsine Sect. *Siebera* (Hoppe) Pax in Engler & Prantl, Natürl. Pflanzenfam. **3** (1b), 83 (1889).

Minuartia Sect. *Siebera* (Hoppe) Graebner in Ascherson & Graebner, Syn. Mitt.-Eur. Fl. **5** (1), 752 (1918) (“Section” cf. p. 700).

Minuartia Sect. *Someraueria* (Hoppe) Mattf. in Bot. Jahrb. **57** Beibl. No. **126**, 31 (1921).

Type: *M. aretioides* (Somerauer) Schinz & Thell. in Bull. Herb. Boiss. ser. 2, **7**, 403 (1907) (= *M. cherlerioides* (Hoppe) Becherer (1956)).

A section of one species, a tetramerous derivative of Section *Lanceolatae*.

The specific nomenclature has been greatly confused, chiefly on account of the first effective publication being, so far as is known, in the “correspondence columns” of “Flora” (1819). As Becherer (1956) has pointed out the basionym of *M. aretioides* (*Arenaria aretioides*) is invalid, not being accepted by the author who published it (Somerauer in his letter). Thus *Siebera cherlerioides* described by Hoppe in his reply (based on a different plant) is the earliest validly published name and so Becherer’s new combination, *M. cherlerioides* is the correct name for the species.

E. Sectio Sclerophylla Mattf. in Fedde Rep. Beih. **15**, 22 (1922).

Lectotype: *M. michauxii* (Fenzl) Mattf. in Bot. Jahrb. **57** Beibl. No. **126**, 28 (1921) (Series *Michauxiae* Mattf.).

Other species:

M. caroliniana (Walt.) Mattf. (1921) (Series *Carolinianae* Mattf.).

M. dawsonensis (Britton) House (1921) (= *M. michauxii* fide Maguire, 1951).

M. nuttallii (Pax) Briq. (1911) (= *M. pungens* (Nutt.) Mattf.) (Series *Pungentes* Mattf.).

?*Arenaria filiorum* Maguire (1946) (aff. *M. nuttallii*).

?*Arenaria macrantha* (Rydb.) Nels. (1909).

?*Arenaria rosei* Maguire & Barneby (1956).

A section of three to six species in eastern and western North America (chiefly U.S.A.). The three species known to Mattfeld were each placed by him in monotypic series. They are very distinct species and the section appears rather heterogeneous. As no material of *Arenaria filiorum*, *A. macrantha* or *A. rosei* has been seen, new combinations in *Minuartia* are not proposed, meanwhile.

Special references: Maguire (1946a), (1951).

F. Sectio Acutiflorae (Fenzl) Hayek, Fl. Steierm. **1**, 274 (1908).

Syn.: *Alsine* 6. *Acutiflorae* Fenzl in Endlicher, Gen. Pl. 965 (1840).

Alsine Sect. *Acutiflorae* (Fenzl) Fenzl in Ledeb., Fl. Ross. **1**, 350 (1842).

Alsine f. "*Calalsine*" Endlicher, Enchir. Bot. 505 (1843), nomen.

Lectotype: *M. austriaca* (Jacq.) Hayek, Fl. Steierm. **1**, 274 (1908).

Section *Acutiflorae* as a whole comprises about fifteen species distributed throughout Central Europe and Central and South-west Asia. The specific limits are very obscure in many cases.

F. (i). Series Acutiflorae

Syn.: *Neumayera* Reichb. [Repert. Herb. Nomencl. 205 (Jul. 1841)–nomen], Ic. Fl. Germ. **5**, 30 (1841).

Minuartia Sect. *Acutiflorae* Series *Flaccidae* Mattf. in Fedde Rep. Beih. **15**, 148 (1922).

Minuartia Sect. *Acutiflorae* Series *Juniperinae* Mattf. l.c. p. 148 (1922) – diagn. in clave.

Species:

M. afghanica Rech. f. (1951)

M. aucheriana (Boiss.) Bornm. (1910)

M. austriaca (Jacq.) Hayek (1908) (type)

M. biebersteinii (Rupr.) Schischk. (1928)

M. flaccida (All.) Schinz & Thell. (1907)

M. glandulosa (Boiss. & Huet) Bornm. (1940)

M. gracilis McNeill (1961)

M. gracilipes (Komarov) Komarov (1936)

M. helmii (Fisch. ex Ser.) Schischk. (1928)

M. jacutica Schischk. (1936)

M. juniperina (L.) Maire & Petitm. (1908)

M. kashmirica (Edgew.) Mattf. (1921)

M. kryloviana Schischk. (1930)

M. lineata Bornm. (1910)

M. litwinowii Schischk. (1936)

M. subuniflora (Alb.) Woronow (1914)

M. taurica (Stev.) Schischk. (1936)

A series of about eleven to sixteen species occurring on the mountains of Central Europe and Central Asia from the Pyrenees to the Himalayas—extending southwards into the steppe lands of South-west Asia. Mattfeld's separation of the more xerophytic species into a separate series (Series *Juniperinae*) cannot be maintained as a complete gradation exists in a number of different areas (notably in the Caucasus and Armenia and in Afghanistan).

F. (ii). Series *Pichleriae* Mattf. in Fedde Rep. Beih. 15, 148 (1922).

Type: *M. pichleri* (Boiss.) Maire et Petitm., Étude Pl. Graec. 4, 49 (1908).

Other species:

M. rimarum (Boiss. & Bal.) Mattf. (1921).

Mattfeld based the Series *Pichleriae* on *M. pichleri*, a species endemic to the Peloponnese, but it is clear that *M. rimarum* which he placed in his Series *Flaccidae* should be included with it. *M. rimarum* which is widely distributed throughout Southern and Eastern Anatolia shows some resemblance to *M. umbellulifera* (Series *Umbelluliferae*) but differs in the more spreading equally three-nerved leaves. Series *Pichleriae* holds an intermediate position between the Series *Acutiflorae* and *Umbelluliferae*.

F. (iii). Series *Umbelluliferae* McNeill, nom. nov.

Syn.: *Minuartia* Sect. *Acutiflorae* Series *Heldreichianae* Mattf. in Fedde Rep. Beih. 148 (1922), quoad descr. excl. *M. heldreichiana* vera.

Type: *M. umbellulifera* (Boiss.) McNeill **comb. nov.**: *Alsine umbellulifera* Boiss., Diagn. Pl. Orient. ser. 2, 5, 61 (1856).

A series of probably only one polymorphic species confined to the Caucasian and Anatolian mountains.

G. Sectio *Tryphane* (Fenzl) Hayek, Fl. Steierm. 1, 271 (1908).

Syn.: *Alsine* 3 *Tryphane* Fenzl in Endlicher, Gen. Pl. 965 (1840), pro parte.

Tryphane (Fenzl) Reichb., Repert. Herb. Nomencl. 205 (1841).

Alsine Sect. *Tryphane* (Fenzl) Fenzl in Ledeb. Fl. Ross. 1, 346 (1842).

Minuartia Sect. *Polymechana* Mattf. in Fedde Rep. Beih. 15, 169-170 (1922).

Lectotype: *M. verna* (L.) Hiern in J. Bot. Lond. 37, 320 (1899) cf. Boiss., Fl. Or. 1, 670 (1867).

Other species names (cf. also lists in Hayek, 1922, Mattfeld, 1922 and Graebner, 1918):

M. attica (Boiss. & Sprun.) Vierh. *M. oxypetala* (Woloszcz.) Kulcz. (1914) (1921)

M. decandra (Reichb.) Fritsch *M. rubella* (Wahlb.) Hiern (1899) (1909) *M. zarecznyi* (Zapal.) Klovov

?*M. facchinii* (Reichb.) Fritsch (1909) (1952)

A section comprising one highly polymorphic species complex widely distributed throughout Eurasia and North America and extending southward onto the mountains of the Mediterranean region. There are probably at least three, and not more than ten, good species in the group.

For nomenclature of this section see under Sect. *Plurinerviae* above (p. 143).

H. Sectio *Alsinanthe* (Fenzl) Graebner in Ascherson & Graebner, Syn. Mitt.-Eur. Fl. 5 (1), 771 (1918).

Syn.: *Alsine* 11. *Alsinanthe* Fenzl in Endlicher, Gen. Pl. 965 (1840), non *Alsinanthus* Desv. (1816).

Alsinanthe (Fenzl) Reichenb., Repert. Herb. Nomencl. 205 (Jul. 1841) et Ic. Fl. Germ. 5, 29, t.209 (1841).

Alsine Sect. *Alsinanthe* (Fenzl) Fenzl in Ledeb., Fl. Ross. 1, 356 (1842).

Lectotype: *M. stricta* (Sw.) Hiern in J. Bot. Lond. 37, 320 (1899).

Other species:

M. elegans (Cham. & Schlecht.) *M. rossii* (R.Br.) Graebn. (1918)
Schischk. (1936) (= *M. rolfii* Nannfeldt (1954))

A section of two or three species with a holarctic distribution, but occurring in the Alps and on the mountains of C. Asia.

Special references: Maguire (1958), Nannfeldt (1954).

J. Sectio *Uninerviae* (Fenzl) Mattf. in Bot. Jahrb. 57 Beibl. No. 126, 28 (1921).

Syn.: *Alsine* 12. *Uninerviae* Fenzl in Endlicher, Gen. Pl. 965 (1840).

"*Mononeuria*" Reichenb., Repert. Herb. Nomencl. 205 (1841), nomen.

?*Alsine* m. "*Alsinocarpus*" Endlicher, Enchir. Bot. 505 (1843), nomen.

Lectotype: *M. patula* (Michx.) Mattf. in Bot. Jahrb. 57 Beibl. No. 126, 28 (1921).

Other species:

M. brevifolia (Nutt.) Mattf. (1921) (= *M. uniflora* fide Maguire, 1951).

M. glabra (Michx.) Mattf. (1921) (= *M. groenlandica* fide Maguire, 1951).

M. groenlandica (Retz) Ostenf. (1920).

M. drummondii McNeill.*

M. uniflora (Walt.) Mattf. (1921).

?*Arenaria muriculata* Maguire (1951) (aff. *M. patula*).

An eastern North American section, extending to Greenland, comprising about six annual species.

K. Sectio *Greniera* (Gay) Mattf. in Bot. Jahrb. 57 Beibl. No. 126, 27 (1921)

Syn.: *Greniera* J. Gay in Ann. Sci. Nat. ser. 3, 4, 27 (1845).

Lectotype: *M. douglasii* (Fenzl) Mattf. in Bot. Jahrb. 57 Beibl. No. 126, 27 (1921).

Other species: *M. howellii* (Wats.) Mattf. (1921).

Excluded species:

Greniera tenella (Nutt.) Torrey (1858) (*Minuartia* Series *Sabulina*).

* *M. drummondii* McNeill, nom. nov.: *Stellaria nuttallii* Torrey et Gray, Fl. N. Amer. 1, 183 (1838).

Cet. syn.:

"*Alsine drummondii*" Fenzl ined.; Torrey & Gray, Fl. N. Amer. 1, 675 (1840), pro syn. *Alsine nuttallii* (Torr. & Gray) Gray, Gen. Pl. U.S. 2, 34 (1842).

Alsinopsis nuttallii (Torr. & Gray) Small, Fl. S.-E. U.S. 420 (1903).

Minuartia nuttallii (Torr. & Gray) Mattf. in Bot. Jahrb. 57 Beibl. No. 126, 28 (1921), non (Pax) Briquet (1911).

Arenaria nuttallii (Torr. & Gray) Stemen & Myers, Oklahoma Fl. 140 (1937), non Pax (1893).

A section comprising two annual species confined to western North America.

L. Sectio *Minuartia*

Syn.: *Alsine* §5. *Minuartiae* * *Perennes* Boiss., Fl. Orient. 1, 679 (1867) [= Series *Leucocephalae* & *Setaceae*].

Alsine § 5. *Minuartiae* ** *Annuae* Boiss l.c. 681 (1867) [= Subsect. *Minuartia* & Subsect. *Xeralsine* Series *Campestres* & *Xeralsine*].

Minuartia §§ *Euminuartia* * *Annuae* (Boiss.) Graebn. in Aschers. & Graebn., Syn. Mitt.-Eur. Fl. 5 (1), 710 (1918).

Minuartia §§ *Euminuartia* ** *Perennes* (Boiss.) Graebn. l.c. (1918).

L. a. Subsectio *Minuartia*

L. a. (i). Series *Montanae* Mattf. in Fedde Rep. Beih. 15, 53 (1922).

Lectotype: *M. montana* L., Sp. Pl. 90 (1753).

Other species:

M. akinfjewii (Schmalh.) Woronow (1914)

M. meyeri (Boiss.) Bornm. (1910)

M. decipiens (Fenzl) Bornm. (1914)

M. multinervis (Boiss.) Bornm.

M. globulosa (Labill.) Schinz & Thell. (1907)

(1915)

M. sandwithii Maire & Simpson (1949)

M. intermedia (Boiss.) Hand.-Mzt. (1912)

M. sintenisii (Lindb.) Rech. f. (1951)

A series of eight xerophytic annual species centred in the Eastern Mediterranean region but extending eastward to northern India and occurring in Spain and western N. Africa (a subsp. of *M. montana*).

L. a. (ii). Series *Minuartia*

Syn.: *Queria* L., Sp. Pl. 90 (1753) et Gen. Pl. ed. 5, 100 (1754).

Minuartia Sect. *Euminuartia* Series *Hispanicae* Mattf. in Fedde Rep. Beih. 15, 53 (1922).

Species:

M. dichotoma L. (1753) (type) (= *M. hispanica* sec. Mattf.)

M. hamata (Hausskn.) Mattf. (1921) (= *Queria hispanica* L.)

M. sclerantha (Fisch. & Mey.) Thell. (1912)

The type series comprises the three most highly specialised annual members of the genus, all native in the Mediterranean region. *M. hamata* with its recurved fruiting bracts has a very distinctive facies and is often maintained in a separate monotypic genus (*Queria hispanica*). In fact, as Mattfeld (1922 p. 69) has pointed out, it is merely a reduced derivative of *Minuartia* and is very close to *M. dichotoma* the type species of the genus.

L. b. Subsectio *Xeralsine* (Fourr.) McNeill, stat. nov.

Syn.: *Xeralsine* Fourr. in Ann. Soc. Linn. Lyon. ser. 2, 16, 347 (1868).

Lectotype: *M. fasciculata* (L.) Reichb., Ic. Fl. Germ. 5, 28 (1841).

L. b. (i). Series *Leucocephalae* Mattf. in Fedde Rep. Beih. 15, 54 (1922).

Type: *M. leucocephala* (Boiss.) Mattf. in Bot. Jahrb. 57 Beibl. 126, 30 (1921).

A series of one perennial species on the Taurus mountains in Turkey.

L. b. (ii). Series *Setaceae* Mattf. in Fedde Rep. Beih. 15, 54 (1922).

Syn.: *Chetropis* Rafin., Fl. Tellur. 3, 80 (1837).

Lectotype: *M. setacea* (Thuill.) Hayek, Fl. Steierm. 1, 271 (1908).

Other species (and species names):

- M. abchasica* Schischk. (1937)
- M. adenotricha* Schischk. (1937)
- M. anatolica* (Boiss.) Woronow (1914)
- M. aucta* Klokov (1947)
- M. bosniaca* (Beck) Maly (1908)
- M. buschiana* Schischk. (1936)
- M. confusa* (Boiss.) Maire & Petitm. (1908)
- M. corymbulosa* (Boiss. & Bal.) McNeill*
- M. erythrosepala* (Boiss.) Hand.-Mzt. (1912)
- M. filifolia* (Forsk.) Mattf. (1921)
- M. granuliflora* (Fenzl) Grossh. (1930)
- M. innominata* McNeill (1962)
- M. krascheninnikovia* Schischk. (1937)
- M. lanuginosa* (Coste) Braun-Blanquet (1931)

- M. leiosperma* Klokov (1937)
- M. leucocephaloides* (Bornm.) Bornm. (1915)
- M. libanotica* (Boiss.) Bornm. (1914)
- M. micrantha* Schischk. (1936)
- M. mutabilis* (Lapeyr.) Schinz & Thell. ex Becherer (1938) (= *M. rostrata* (Pers.) Reichb. (1842))
- M. parvulorum* Rech. f. (1951) incl. *M. antilibanotica* McNeill (1961)
- M. stereoneura* Mattf. (1922)
- M. tchihatcheffii* (Boiss.) Hand.-Mzt. (1912)
- M. tenuissima* (Pomel) Mattf. (1922)
- M. thyraica* Klokov (1947)
- M. woronowii* Schischk. (1936)

A series of about eighteen perennial species in C. Europe and the Mediterranean region (incl. Anatolia and the Caucasus).

L. b. (iii). Series *Xeralsine*

Syn.: *Minuartia* Sect. *Euminuartia* Series *Fasciculatae* Mattf. in Fedde Rep. Beih. 15, (1922).

Species:

- M. fasciculata* (L.) Reichb. (1842) (type)
- M. funkii* (Jord.) Graebn. (1918)
- M. glomerata* (M.B.) Degen (1910)

Excluded species:

- M. urumiensis* (Bornm.) Bornm. (Section & Series *Sabulina*).

A series of three usually biennial species on the mountains of Southern Europe, extending into N. Africa.

L. b. (iv). Series *Campestres* Mattf. in Fedde Rep. Beih. 15, 54 (1922).

Type: *M. campestris* L., Sp. Pl. 89 (1753).

A series of one annual species in Spain and North Africa.

M. Sectio *Sabulina* (Reichb.) Graebn. in Aschers. & Graebn., Syn. Mitt.-Eur. Fl. 5 (1), 700 (1918).

Syn.: *Sabulina* Reichb., Fl. Germ. Excurs. 785 (1832), pro parte.

Alsine 1. *Sabulina* (Reichb.) Fenzl in Endlicher, Gen. Pl. 964 (1840) ("*Sabulineae*").

Alsine Sect. *Sabulina* (Reichb.) Fenzl in Ledeb., Fl. Ross. 1, 342 (1842) ("*Sabulineae*").

* *Minuartia corymbulosa* (Boiss. et Bal.) McNeill, comb. nov.: *Alsine corymbulosa* Boiss. et Bal. in Boiss., Diagn. Pl. Orient. ser. 2, 6, 36 (1859), non Bor. (1859)-nom. provis.

Lectotype: *Minuartia tenuifolia* (L.) Hiern in J. Bot. Lond. **37**, 321 (1889), non Nees ex Mart. (1814). (cf. Fenzl in Endlicher l.c.).

M. (i). Series *Sabulina*

Syn.: *Minuartia* Sect. *Sabulina* Series *Tenuifoliae* Mattf. in Fedde Rep. Beih. **15**, 32 (1922).

Species (and species names):

- | | |
|--|--|
| <i>M. bilykiana</i> Klovov (1952) | <i>M. piskunovii</i> Klovov (1952) |
| <i>M. birjuczensis</i> Klovov (1947) | <i>M. regeliana</i> (Trautv.) Mattf. (1921) |
| ? <i>M. densiflora</i> (Vis.) Fritsch (1909) | <i>M. subtilis</i> (Fenzl) Hand.-Mzt. (1912) |
| <i>M. hybrida</i> (Vill.) Schischk. (1936) (incl. <i>M. tenuifolia</i> (L.) Hiern (1899)—type) | ? <i>M. tenella</i> Mattf. (1921) |
| <i>M. hypanica</i> Klovov (1947) | <i>M. thymifolia</i> (Sibth. & Sm.) Bornm. (1914) |
| <i>M. mediterranea</i> (Ledeb.) Maly (1908) | <i>M. urumiensis</i> (Bornm.) Bornm. (1915) |
| <i>M. mesogitana</i> (Boiss.) Hand.-Mzt. (1912) | <i>M. viscosa</i> (Schreb.) Schinz & Thell. (1907) |

A series of nine or ten annual species centred in S. Europe and the Mediterranean area. Mattfeld (1922) included one species in North America (*M. tenella*) but Maguire (1951, 1958) regards this as a subspecies of *M. michauxii* (as *Arenaria stricta* Michx. subsp. *macra* (Nels. & Macbr.) Maguire) in Section *Sclerophylla*; no authentic material has been seen. The European and Orient forms are highly polymorphic and many named taxa have been described

M. (ii). Series *Californicae* Mattf. in Fedde Rep. Beih. **15**, 30 (1922).

Syn.: *Alsine* 9. *Saginella* Fenzl in Endlicher, Gen. Pl. 964 (1840).

Saginella (Fenzl) Reichb., Repert. Herb. Nomencl. 205 (1841).

Alsine Sect. *Saginella* (Fenzl) Fenzl in Ledeb., Fl. Ross, **1**, 356 (1842) ("*Saginellae*").

Type: *M. californica* (Gray) Mattf. in Bot. Jahrb. **57** Beibl. No. **126**, 28 (1921).

Other species:

M. acutiflora (Fenzl) Mattf. (1921) *M. pusilla* (Wats.) Mattf. (1921)

A series of three annual species, two in California and one in Chile.

(1931) 12. 24. April 7. *Lepyrodiclis* Fenzl

Lepyrodiclis Fenzl in Endlicher, Gen. Pl. 966 (1840); Pax & Hoffmann in Engler & Harms, Natürl. Pflanzenfam. ed. 2, **16c**, 333 (1934).

Syn.: *Arenaria* Subgenus vel Sectio *Lepyrodiclis* (Fenzl) Benth. in Benth. & Hook. f., Gen. Pl. **1**, 150 (1862).

Arenaria Sect. *Lepyrodiclis* (Fenzl) Edgeworth & Hook. f. in Hook. f., Fl. Brit. Ind. **1**, 241 (1874).

Type: *L. holosteoides* (C. A. Mey.) Fenzl ex Fisch. & Mey., Enum. Pl. nov. Schrenk **1**, 110 & 93 (1841).

Other species:

L. stellarioides Schrenk ex Fisch. *L. tenera* Boiss. (1853).
& Mey. (1841).

Excluded species:

L. giralddii Diels = *Arenaria giralddii* (Diels) Mattf. (Subgenus *Odontostemma*).

L. paniculata Stapf (*Ar. holosteoides* δ *paniculata* (Stapf) Wms.) = *Stellaria kotschyana* Fenzl ex Boiss.

L. quadridentata Maxim. = *Arenaria quadridentata* (Maxim.) Williams (Subgenus *Odontostemma*).

A genus of three species extending across Asia from Eastern Turkey and the Caucasus to western Tibet and the western Himalayas (cf. fig. 5).
Special reference: Wagenitz (1957).

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