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A biometric study of the *Arenaria ciliata* L. complex (Caryophyllaceae)

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ABSTRACT

25 morphological characters were recorded for 178 herbarium specimens belonging to the *Arenaria ciliata* L. complex. Multivariate analysis suggested that they be referred to three species, *A. ciliata* L., *A. norvegica* Gunnerus and *A. gothica* Fries. *A. moehringioides* J. Murr was included as a subspecies of *A. gothica*. *A. gothica* subsp. **moehringioides** (J. Murr) M. B. Wyse Jackson & J. Parnell, **comb. nov.** Plants of *A. gothica* subsp. *gothica* from Sweden and Switzerland were found to be morphologically distinct and were treated as varieties i.e. *A. gothica* subsp. *gothica* var. *gothica* for the Swedish plants and *A. gothica* subsp. *gothica* var. **fugax** (Gay ex Gren.) M. B. Wyse Jackson & J. Parnell, **comb. nov.** for the Swiss plants.

Four of the five subspecies of *A. ciliata* recognized by Jalas & Suominen (1983) were maintained, as was the variety *A. ciliata* subsp. *ciliata* var. *hibernica* (Ostenf. & O. C. Dahl) G. C. Druce. Multivariate analysis confirmed the inclusion of *A. ciliata* subsp. *bernensis* in *A. ciliata* sensu stricto and not *A. gothica* subsp. *moehringioides* as had been previously suggested.

A. ciliata subsp. *polycarpoides* (Rouy & Fouc.) Br.-Bl. was seen to intergrade with *A. gothica* subsp. *moehringioides* and does not warrant separate status.

INTRODUCTION

Arenaria L. is a medium sized genus of about 160 species which occurs mainly in arctic and temperate regions of the northern hemisphere. It is usually placed in the sub-family Alsinoideae of the Caryophyllaceae. This sub-family is characterized by its opposite leaves, absence of stipules, usually well-developed petals and free or only partly fused sepals. In the most recent comprehensive treatment, McNeill (1962) split *Arenaria* into ten subgenera, the most widespread of which is subgenus *Arenaria*. This contains eleven sections including the pan-arctic section *Rariflora* Williams, the type species of which is *Arenaria ciliata* L.

A. ciliata sensu lato has a confused taxonomic history. The very wide variation both in morphology and in the level of ploidy together with geographic isolation has led to the evolution of a number of closely related taxa which together form the so-called *A. ciliata* complex. The complex has been taken to include as many as seven and as few as two species. However as a basis for this study we follow Hess, Landolt & Hirzel (1967) and take it to include the four species *A. ciliata* sensu stricto, *A. moehringioides* Murr (= *A. multicaulis* L.), *A. norvegica* Gunnerus and *A. gothica* Fries.

A. ciliata s.s. occurs through the Alps, the Tatra (as subsp. *tenella* (Kit.)Br.-Bl.) in the Carpathians, the northern Apennines and with single stations in the Dinaric (western-central Yugoslavia) and northern Albanian Alps. North of the Tatra it occurs only in north-western Ireland (subsp. *hibernica* Ostenf. & O. C. Dahl) and, as subsp. *pseudofrigida* Ostenf. & O. C. Dahl, in Finland, Norway (extreme north), Spitzbergen, the Russian arctic and eastern Greenland. *A. moehringioides* has a more western distribution than *A. ciliata* s.s., occurring in northern Spain, the Pyrenees, Jura, and Alps to Vorarlberg and northern Italy. *A. norvegica* is a northern species occurring throughout Iceland and scattered through the mountains of Norway and northern Sweden. It also occurs in Shetland, Scotland and western Ireland. The Irish station is the southernmost for the species (53°N), but it has not been seen there for 25 years. *A. norvegica* is also found in western Yorkshire in England as subsp. *anglica* Halliday. *A. gothica* is a species with a very disjunct distribution. It occurs in southern mainland Sweden and on the island of Gotland and also in the Swiss Jura. All members of the complex are mountain plants, except for the lowland *A. gothica*, which mostly grow in open habitats on base-rich soils.

A. ciliata s.s. is a low-growing herbaceous chamaephyte which characteristically has small (<10 mm long), entire, non-fleshy, oblanceolate or spathulate leaves which are ciliate at least at the base. The flowers are usually solitary or paired (rarely in threes), with white petals that are 1·5–2 times as long as the sepals.

Despite the splitting of the *A. ciliata* complex, *A. ciliata* s.s. remains a very polymorphic species. Thus it in turn has been divided into a number of geographically disjunct subspecies. Jalas & Suominen (1983), for example, recognize the following: *A. ciliata* subsp. *ciliata*, subsp. *bernensis* Favarger, subsp. *hibernica* Ostenf. & O. C. Dahl, subsp. *pseudofrigida* Ostenf. & O. C. Dahl and subsp. *tenella* (Kit.) Br.-Bl.

The first two subspecies, *A. ciliata* subsp. *bernensis* and subsp. *ciliata*, are in fact the only two subspecies which have partially overlapping ranges, both occurring in the Bernese Alps in Switzerland. Favarger (1960, 1963) separated the former from subsp. *ciliata* on morphological, cytological and ecological differences. However the occurrence of some intermediate populations has led Jalas & Suominen (1983) to question their separate status.

The other subspecies of *A. ciliata* s.s. have also posed taxonomic problems. Halliday (1960a) recognized that subsp. *pseudofrigida* and subsp. *tenella* are morphologically very similar. They also have the same chromosome number of $2n = 40$ (Horn 1948; Favarger 1963). In their turn, other workers have noted that these two subspecies are similar to subsp. *ciliata* and subsp. *hibernica* (see Clapham 1962; Chater & Halliday 1964).

It is clear that although the *A. ciliata* complex has been split into a number of taxa the distinctions between them are still somewhat unclear. Our aim was to try to clarify the variation pattern of the complex in general, whilst concentrating especially on four subspecies of *A. ciliata* s.s., i.e. subsp. *bernensis*, subsp. *ciliata*, subsp. *hibernica* and subsp. *pseudofrigida*.

Despite the obviously complex nature of the variation pattern shown by the *A. ciliata* complex, all previous accounts of it have relied on orthodox taxonomic techniques. We felt that a new approach was needed. The approach we chose involved the use of multivariate statistics to analyze measurements made on herbarium specimens.

MATERIALS AND METHODS

178 pressed specimens of the above four species were identified using the appropriate regional Floras and scored for 25 morphological characters (Table 1, Fig. 1). The characters chosen were a combination of those used in appropriate local Floras or descriptions of the taxa, together with characters which we felt would give optimal species or subspecies separation.

Some characters measured were found not to be as useful as initially hoped. Characters 19–25 (see Table 1) are qualitative and can thus only be used in a multivariate analysis in averaged or percentage form to show general tendencies in the data. Character 15 (seed length) could not be recorded for all plants examined and so is only used when average values are being considered. The ratios (Characters 16–18) were found, like Characters 19–25, to be useful only in expressing the broadest variation patterns in the data. The only specimen of *A. ciliata* subsp. *tenella* that we saw was too young to be of use in this study. Measurements of *A. norvegica* subsp. *anglica* were made on a single cultivated specimen in the Trinity College Botanic Garden (Dublin). This taxon was included only in the analysis presented in Fig. 4.

The data were standardised for use in a principal components analysis (PCA) program (BMDP4M). Bivariate scatter diagrams showing the morphological relationships of the plants scored are shown in Figs. 2, 3, 4 & 5. These scatters form the basis for all further discussion of the *A. ciliata* complex in this paper.

RESULTS AND DISCUSSION

Not all of the characters measured were equally useful at all stages of the analysis. Thus, where very general trends in the data were being considered and where the data were or could be

TABLE 1. MORPHOLOGICAL CHARACTERS RECORDED FOR MULTIVARIATE ANALYSES
The figures in brackets refer to the number of measurements made for each character on each specimen. See Fig. 1 for illustrations of some of the characters.

1. Petal length (3)
2. Sepal length (3)
3. Leaf length (3)
4. Leaf width (3)
5. Flower diameter (3)
6. Pedicel length (3)
7. No. of flowers per cyme (3)
8. Maximum length of flowering shoot (1)
9. No. of flowering shoots (1)
10. No. of sterile shoots (1)
11. No. of styles per flower (3)
12. No. of capsule teeth (3)
13. Length of leaf ciliation (3)
14. Length of sepal ciliation (3)
15. Seed length (5)
16. Petal length/Sepal length
17. Leaf length/Leaf width
18. Pedicel length/Sepal length
19. Plants perennial or annual
20. Lateral nerves of leaf conspicuous or not (3)
21. Lateral nerves of sepals conspicuous or not (3)
22. Backs of sepals pubescent or not (3)
23. Leaf midrib distinct or not (3)
24. Stems pubescent or not (3)
25. Pedicels pubescent or not (3)

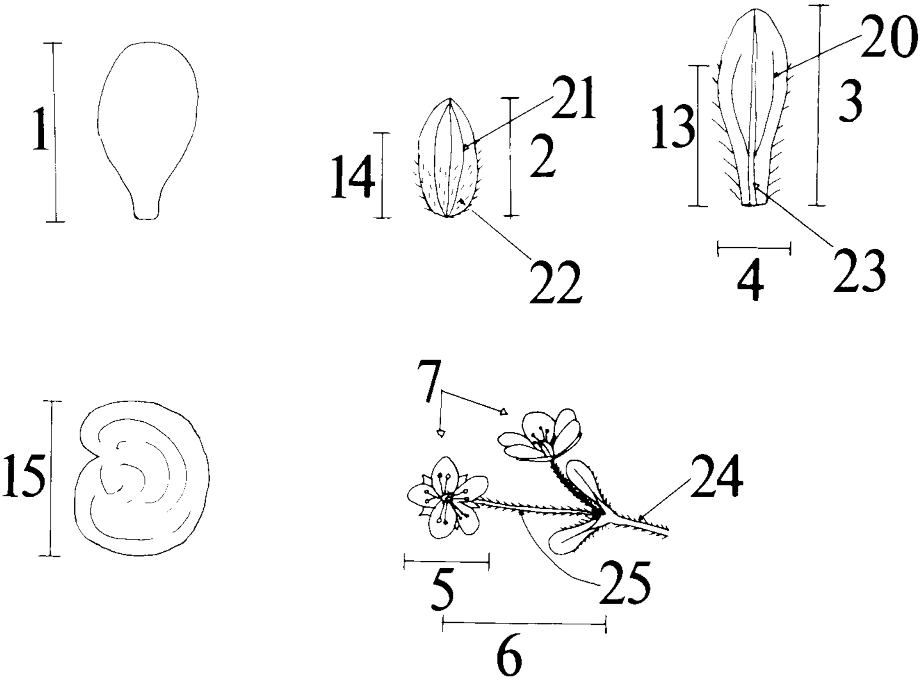

FIGURE 1. Some of the characters used in the multivariate analyses. Top row l.–r.: Petal, Sepal, Leaf. Bottom row l.–r.: Seed, Inflorescence of *A. ciliata* s.s.

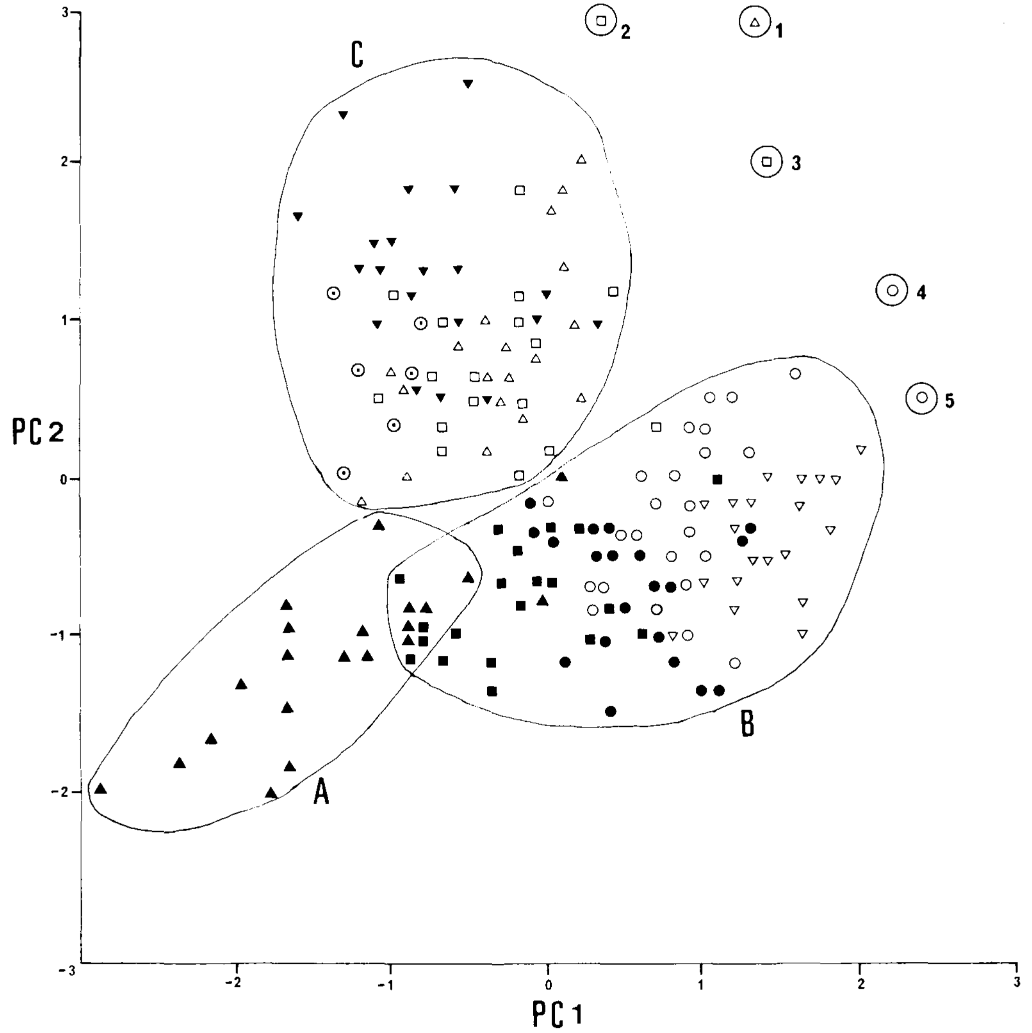

FIGURE 2. Principal Components Analysis of individual specimens (excluding *A. norvegica* subsp. *anglica*) in the *A. ciliata* complex. Components 1 (PC1) and 2 (PC2) are illustrated. PC1 accounts for 26·2% of the variation and PC2 for 16·5%. ⊙ = *A. ciliata* subsp. *polycarpoides*, ○ = *A. ciliata* subsp. *hibernica*, ■ = *A. ciliata* subsp. *pseudofrigida*, ● = *A. ciliata* subsp. *ciliata*, ▽ = *A. ciliata* subsp. *bernensis*, ▲ = *A. norvegica* subsp. *norvegica*, ⊽ = *A. norvegica* subsp. *anglica* (only on Fig. 4), □ = *A. moehringioides*, ▼ = *A. gothica* (Switzerland), △ = *A. gothica* (Sweden)

considered as percentage or mean data, all 25 characters were used in the analysis (Fig. 4). Where this was not the case, only the unmeaned data for characters 1–14 were used (Figs. 2, 3 & 5).

GENERAL PATTERN OF VARIATION

Fig. 2 shows the first two Components of the PCA of all 178 individuals in the *A. ciliata* complex. Aberrant individuals, usually of exceptional size, lie in the top right of the scatter (numbered 1–5) and are not further discussed. Fig. 3 shows Components 1 and 3 of the PCA of all 178 individuals in the complex. Based on these results there is little evidence for strong distinctions between any of

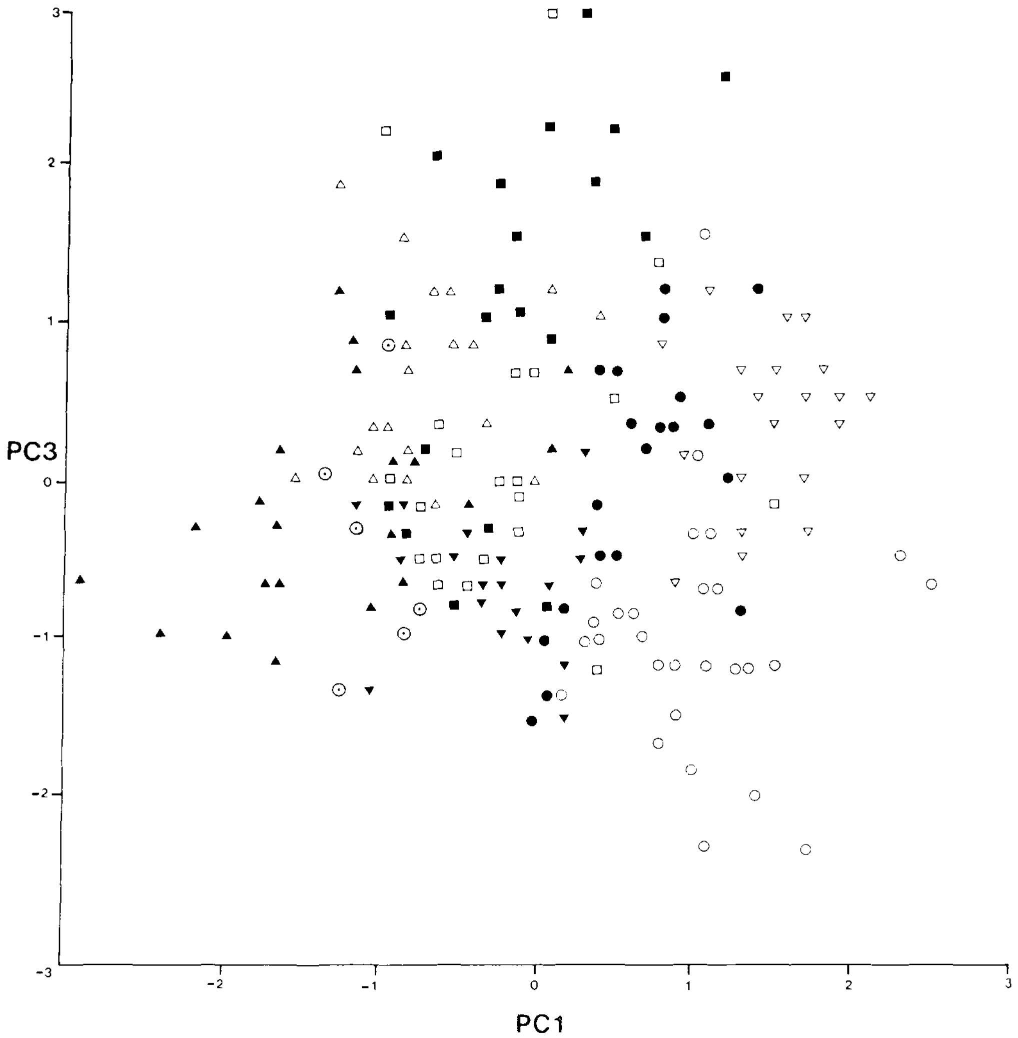

FIGURE 3. Principal Components Analysis of individual specimens (excluding *A. norvegica* subsp. *anglica*) in the *A. ciliata* complex. Components 1 (PC1) and 3 (PC3) are illustrated. See Fig. 2 for explanation of symbols. PC1 accounts for 26·2% of the variation and PC3 for 13·0%.

the species or subspecies. This is somewhat surprising as the characters chosen are those that are usually used to distinguish taxa in the complex, indicating that the distinctions between them are not as clearcut as is generally held. However three loose groupings (emphasized in Fig. 2 by the envelopes surrounding them) can be recognized.

Group (A) towards the bottom left corner of Fig. 2 contains virtually all plants assignable to *A. norvegica*. However, though *A. norvegica* is usually recognized as a separate species, it is apparent from this scatter that it shows some morphological overlap with *A. ciliata* subsp. *pseudofrigida*. This overlap is also seen in Fig. 3. These two taxa do, however, mostly lie in different areas of this scatter and are, on the whole, quite distinct.

Group (B) to the right of Group (A) in Fig. 2 is made up almost entirely of plants assignable to *A. ciliata* s.s. This group is discussed in more detail below.

Group (C) in the upper middle part of Fig. 2 contains plants of *A. moehringioides* and *A.*

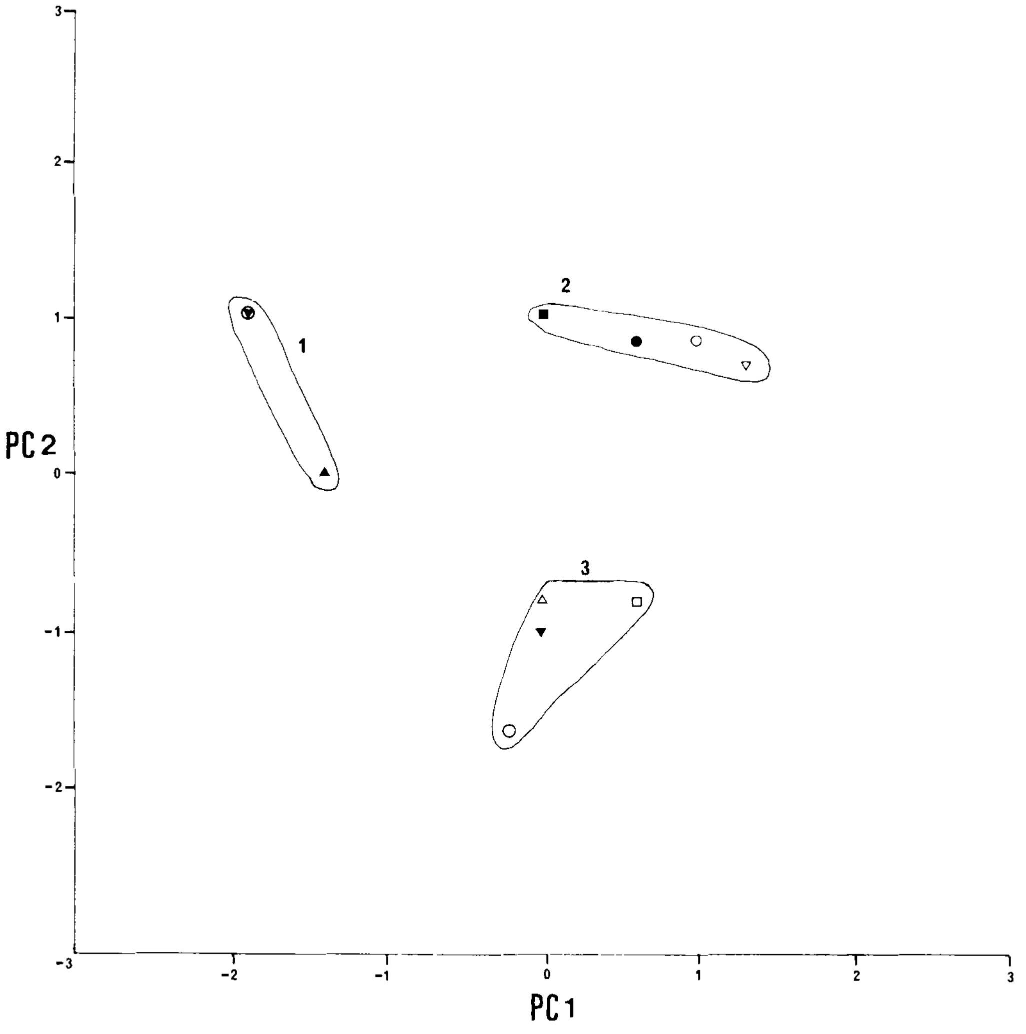

FIGURE 4. Principal Components Analysis of meaned data for all taxa in the *A. ciliata* complex. Components 1 (PC1) and 2 (PC2) are illustrated. See Fig. 2 for explanation of the symbols. PC1 accounts for 28·2% of the variation and PC2 for 20·0%.

gothica. Three points are evident in relation to the scatter of this group. Firstly, it seems impossible to effectively separate *A. moehringioides* and *A. gothica*. This is supported by Fig. 3 in which *A. gothica* from both Sweden and Switzerland grade into *A. moehringioides*. Secondly, *A. ciliata* subsp. *polycarpoides* (Rouy & Fouc.) Br.-Bl. intergrades with typical *A. moehringioides*. This is also seen in Fig. 3 though not as clearly as in Fig. 2. The degree of overlap is large considering the small sample size. We feel that the weight of evidence is against giving *A. ciliata* subsp. *polycarpoides* separate status in *A. moehringioides*. Thirdly, it has been suggested by Rouy & Foucaud (1896), Williams (1898) and Chater & Halliday (1964) that Swiss and Swedish *A. gothica* are significantly different. Chater & Halliday (1964), whose observations were based on cultivated plants, describe Swiss *A. gothica* as being less ciliate and with larger cymes than Swedish plants of the same species. Our analysis supports such a difference. In Fig. 2 only a few plants of Swiss *A. gothica* show morphological overlap with Swedish *A. gothica*. In Fig. 3 Swiss *A. gothica* is in fact almost completely separated from Swedish *A. gothica*.

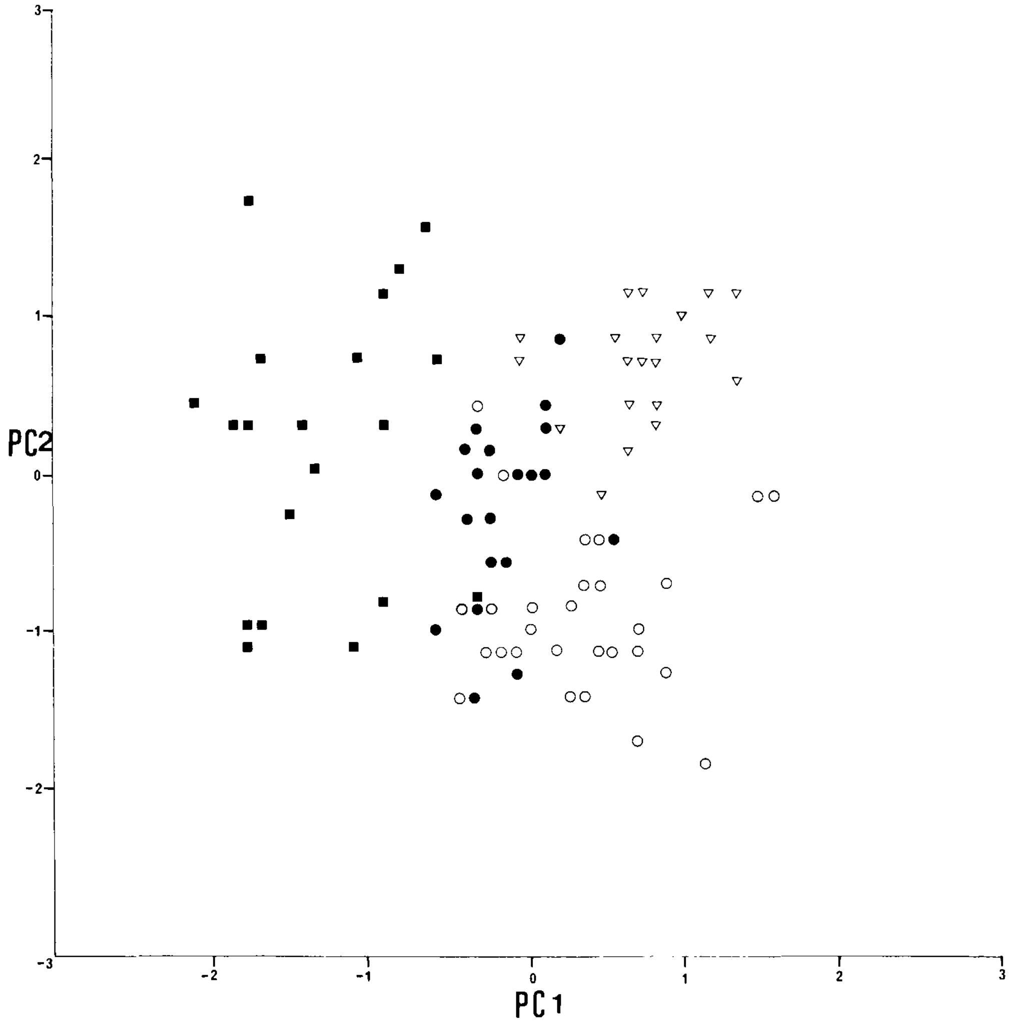

FIGURE 5. Principal Components Analysis of individual specimens of *A. ciliata* s.s. (Group 2 of Fig. 4). Components 1 (PC1) and 2 (PC2) are illustrated. See Fig. 2 for explanation of the symbols. PC1 accounts for 30·7% of the variation and PC2 for 18·3%.

In order to emphasize the differences between the groups (A to C) in Fig. 2, the data for each taxon were meaned and a PCA and a Cluster Analysis (BMDP2M) performed.

Fig. 4 shows the first two Components of the PCA of the meaned data for all taxa measured. A comparison of Figs. 2 & 4 indicates that Fig. 4 emphasizes the differences that occur between and within groups. We use it to illustrate five points. Firstly, there is evidently a clear difference between Group 1 (Fig. 4) and the rest of the complex. So although individuals of *A. norvegica* show some morphological overlap with *A. ciliata* subsp. *pseudofrigida*, on average, these two taxa are distinct. Secondly, within *A. norvegica* s.l., the rare taxon subsp. *anglica* is distinguishable from subsp. *norvegica*. Thirdly, *A. ciliata* s.s. (Group 2 of Fig. 4) can be seen to contain four elements that show a gradation from subsp. *pseudofrigida* through subsp. *ciliata* and subsp. *hibernica* to subsp. *bernensis*. This trend represents a morphological shift from small plants with weakly ciliate leaves, short petals and small seeds to larger plants with large, strongly ciliate leaves, longer petals and larger seeds. Closer inspection of Fig. 2 also reveals the trend, though naturally it is less clear. Fourthly, there is a very clear separation between *A. ciliata* subsp. *bernensis* and *A. moehringioides*. This does not support the suggestion of Welten & Sutter (1982) that the former should be included in the latter. This separation can also be clearly seen in Fig. 2. Finally, *A. gothica* and *A. moehringioides* (Group 3 of Fig. 4) are clearly separated from the rest of the complex; though again these two species are not clearly separable from each other. Component 3 in the PCA of the average values accounts for 16.8% of the variation but does not significantly alter the groupings seen in Fig. 4.

In summary, Figs. 2, 3 & 4 show there to be three principal groups present in the *A. ciliata* complex. The first group contains *A. norvegica* s.l., which may, on average, be distinguished by its weak leaf and sepal ciliation, fleshy leaves, sparse pedicel pubescence and more or less equally long petals and sepals. The second group contains *A. ciliata* s.s. which may, on average, be distinguished by a combination of its large flowers (9·0–14·5(–15) mm in diameter), long petals ((5·0–)6·0–8·0 mm), few flowers per cyme (1–2(–3)), usually strongly ciliate leaves, pubescent pedicels and petals 1·5–2·0 times as long as the sepals. The third group contains *A. moehringioides* and *A. gothica* which may, on average, be distinguished by their small flowers (5·5–8·0(–9) mm in diameter), short petals (3·5–6·0 mm), greater number of flowers per cyme ((2–)3–6(–9)) and leaves c. 2–2·5 times as long as broad. The morphological similarity of these two species is emphasized by the fact that the most striking difference between them (Character 19, Table 1) did not effectively separate them in these analyses. Within this group, *A. moehringioides*, *A. gothica* and *A. ciliata* subsp. *polycarpoides* intergrade and do not warrant separate specific status. These analyses do however support separation of Swiss and Swedish *A. gothica*. The groupings seen in the PCA scatters were confirmed by the Cluster Analysis.

VARIATION OF *A. CILIATA* S.S.

Fig. 5 shows the first two Components of a PCA of individuals of *A. ciliata* s.s. This analysis provides a clearer resolution of the relationships of the subspecies within *A. ciliata* s.s. *A. ciliata* subsp. *ciliata* occupies the centre of the scatter and around it are arranged the other subspecies. Subsp. *bernensis* lies towards the top right hand corner of the scatter and is clearly separable from its nearest neighbours, subsp. *ciliata* and subsp. *hibernica*. *A. ciliata* subsp. *pseudofrigida* is also well separated from the rest of the subspecies, lying as it does on the left-hand side of the scatter and showing little overlap with any of the other taxa. Such clear separation however cannot be said to exist between subsp. *hibernica* and subsp. *ciliata* – there is in fact a significant overlap between them. Certainly these two subspecies are morphologically very similar. This scatter also shows that subsp. *hibernica* can be distinguished from subsp. *pseudofrigida*. We found that subsp. *pseudofrigida* has in comparison with subsp. *hibernica* smaller flowers (c. 9–12 mm in diameter cf. 10–13 mm) and shorter, narrower leaves (3–5 mm × 1–1·5 mm cf. 3·5–6(–7) mm × 1·5–2 mm) which are never (cf. almost always) ciliate to the tip. They are, however, cytologically and chemically very similar. For the Irish plant we obtained a chromosome count identical to Horn's (1948) count of $2n = 40$ for subsp. *pseudofrigida*. (Halliday's (1960a) count for subsp. *hibernica* is reported as $2n =$ c.40 in Clapham (1962).) The results of a chemical analysis that we performed on these two subspecies indicated that they also have an almost identical pattern of leaf flavonoids. However this scatter suggests that these two subspecies are morphologically less closely related to each other than they are to subsp. *ciliata*. Component 3 accounts for 14·0% of the variation but does not significantly alter the groupings seen in Fig. 5.

Halliday (pers. comm.) has indicated the close relationship of *A. ciliata* subsp. *tenella* to subsp. *hibernica*. However, both Kitaibel (1814) and Graebner (1919) describe the former taxon as having leaves ciliate at the base. Based on these descriptions it seems that subsp. *tenella* is probably less closely related to subsp. *hibernica*, which has leaves almost always ciliate to the tip, than it is to subsp. *pseudofrigida* which has leaves ciliate at the base.

CONCLUSION

Multivariate analysis of the *A. ciliata* complex has facilitated the clarification of some of the relationships of the taxa normally included in it. Thus three groups can clearly be recognized: *A. norvegica* s.l., *A. ciliata* s.s. and *A. moehringioides*/*A. gothica*.

A. norvegica s.l. has proved to be closely related to, though distinct from, *A. ciliata* s.s. Two infra-specific taxa corresponding to the two hitherto recognized subspecies of *A. norvegica* have been distinguished in this analysis.

Within the *A. moehringioides*/*A. gothica* group it has proved impossible to separate *A. gothica* from *A. moehringioides*. However, the differences in life-history, chromosome number, habit and geographical distribution of the two taxa warrant their separation at subspecific level. (*A. gothica* is an annual or biennial with 2n = 100 and is taller and more erect than *A. moehringioides*. *A. moehringioides* on the other hand is a perennial with 2n = 40.) This solution is of the same type as that proposed by Halliday (1960b) who included the short-lived *A. gothica* auct. angl. in *A. norvegica* as subsp. *anglica*. Additionally our analysis failed to effectively separate *A. ciliata* subsp. *polycarpoides* from *A. moehringioides* and we think that these two taxa should be considered synonymous. Finally, *A. gothica* has proved to be variable, and the Swiss plants warrant separation from the Swedish plants at the varietal level. Swiss *A. gothica* tends to be taller, to have more flowers per cyme, less ciliate leaves and slightly larger seeds than Swedish *A. gothica*. The former also rarely (cf. commonly) has cilia on the back of the sepals.

Within *A. ciliata* s.s. there is a general trend from subsp. *bernensis* (with parts generally large) to subsp. *pseudofrigida* (with parts generally small). This latter subspecies has proved to be less closely related to subsp. *hibernica* than had been previously thought. This work has also shown that subsp. *hibernica* intergrades with typical subsp. *ciliata* and does not warrant taxonomic recognition at subspecific level.

LIST OF TAXA AND SELECTED SYNONYMY

1. *ARENARIA NORVEGICA* Gunnerus, *Fl. Norvegica*, **2**: 144 (1772).

a. Subsp. *NORVEGICA*
A. ciliata subsp. *norvegica* (Gunnerus) Fries, *Novitiae Florae Suecicae*, 2nd ed., **2**: 34 (1839).

b. Subsp. *ANGLICA* Halliday in *Watsonia*, **4**: 209 (1960).

2. *ARENARIA CILIATA* L., *Sp. Pl.*, 425 (1753).

a. Subsp. *CILIATA*

i. Var. *CILIATA*

ii. Var. *HIBERNICA* (Ostenf. & O. C. Dahl) G. C. Druce in *Rep. botl Soc. Exch. Club Br. Isl.*, **5**: 279 (1919).
Arenaria ciliata L. subsp. *hibernica* Ostenf. & O. C. Dahl, in *Nyt Mag. Naturvid.*, **55**: 216 (1917).

b. Subsp. *BERNENSIS* Favarger in *Ber. schweiz. bot. Ges.*, **73**: 176 (1963).

c. Subsp. *PSEUDOFRIGIDA* Ostenf. & O. C. Dahl in *Nyt Mag. Naturvid.*, **55**: 217 (1917).
A. pseudofrigida (Ostenf. & O. C. Dahl) Juz. ex Schischkin & Knorring in Komarov, *Fl. USSR*, **6**: 537 (1936).

d. Subsp. *TENELLA* (Kit.) Br.-Bl., *Sched. Flor. Raet. exsicc.*, **10**: 279 (1927).
A. multicaulis var. *tatrensis* Zapal., *Consp. Fl. Galic.*, **3**: 42 (1911).
A. ciliata subsp. *tatrensis* (Zapal.) Favarger in *Ber. schweiz. bot. Ges.*, **73**: 174 (1963).

3. *ARENARIA GOTHICA* Fries, *Novitiae Florae Suecicae*, 2nd ed., **2**: 33 (1839).

a. Subsp. *GOTHICA*

i. Var. *GOTHICA*

A. ciliata subsp. *gothica* (Fries) Hartman, *Svensk Norsk Excurs.-Fl.*, 63 (1846).
A. ciliata "forme" *A. gothica* α *gothica* (Fries) Rouy & Fouc., pro parte, *Fl. Fr.*, **3**: 248 (1896).

ii. Var. **FUGAX** (Gay ex Gren.) M. B. Wyse Jackson & J. Parnell, **comb. nov.**
Basionym: *Arenaria ciliata* β *fugax* Gay ex Gren. in Grenier & Godron, *Fl. Fr.*, **1**: 259 (1848).
A. ciliata c. *laxior* Gremli, *Excurs.-Fl. Schweiz*, 3rd ed. 103 (1878).
A. ciliata "forme" *A. Gothica* β *jurana* Genty ex Rouy & Fouc., *Fl. Fr.*, **3**: 248 (1896).

b. Subsp. **MOEHRINGIOIDES** (J. Murr) M. B. Wyse Jackson & J. Parnell, **comb. nov.**
Basionym: *Arenaria moehringioides* J. Murr, *Allg. bot. Z.* **12**: 176 (1906).
A. ciliata L. var. β, *Sp. Pl.* 425 (1753).
A. multicaulis L., *Syst. Nat.* 10th ed. **2**:1034 (1759), pro parte, nom. illeg.
A. ciliata "forme" *A. polycarpoides* Rouy & Fouc., *Fl. Fr.*, **3**: 247 (1896).
A. ciliata subsp. *polycarpoides* (Rouy & Fouc.) Br.-Bl., *Sched. Flor. Raet. exsicc.*, **10**: 279 (1927).
A. ciliata subsp. *moehringioides* (J. Murr) Br.-Bl., *Sched. Flor. Raet. exsicc.*, **10**: 279 (1927).
A. ciliata subsp. *multicaulis* (L.) O. Schwarz, *Mitt. thüring. bot. Ges.*, **1**: 98 (1949), non Arcangeli.

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