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Variation in *Jasione montana* L. (Campanulaceae) and related species in Europe and North Africa

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ABSTRACT

This paper describes the variation of European and North African *Jasione montana* L. North African material is assigned to *J. montana* subsp. *cornuta* Greuter & Burdet. All other *J. montana* belongs to *J. montana* subsp. *montana* within which six varieties are recognized. These are *J. montana* subsp. *montana* var. *montana*, *J. montana* subsp. *montana* var. *litoralis* Fr., *J. montana* subsp. *montana* var. *latifolia* Pugsl., *J. montana* subsp. *montana* var. *echinata* Boiss. & Reuter, *J. montana* subsp. *montana* var. *bracteosa* Willk. and **J. montana** subsp. **montana** var. **imbricans** J. Parnell, **var. nov.** Only the first three of these varieties occur in Britain. A number of *Jasione* species are relegated to synonymy with these taxa though the closely related *J. penicillata* Boiss., *J. corymbosa* Poiret ex Schultes and *J. heldreichii* Boiss. & Orph. are maintained as species. The two latter species are each recognized as containing two varieties; these are *J. corymbosa* var. *corymbosa*, **J. corymbosa** var. **glabra** (Durieu ex Boiss. & Reuter) J. Parnell, **stat. et comb. nov.**, *J. heldreichii* var. *heldreichii* and **J. heldreichii** var. **papillosa** J. Parnell, **var. nov.**

INTRODUCTION

The genus *Jasione* L. (Campanulaceae) contains twelve species. It can be conveniently split into an annual/biennial section and a perennial section. Although two of the perennial members, *Jasione bulgarica* Stoj. & Stefanov and *Jasione foliosa* Cav., have, on occasion, been placed in separate genera, I feel that *Jasione* clearly forms a single natural entity. In this paper I have applied a combination of a detailed, experimental, biometric study of *Jasione montana* L. from the British Isles and herbarium observations of material from elsewhere to re-assess the infraspecific classification and relationship of all non-perennial *Jasione* species.

J. montana is the most widespread species in the genus, occurs commonly throughout Europe, and has an ill-defined pattern of infraspecific variation. Details of its autecology, morphology and distribution are given in Parnell (1985). Plants of this species may be either annual or biennial, may vary from almost glabrous to hirsute, may be branched in the lower half or unbranched and be from 1 to 65 cm tall. Recent revisions vary considerably in their treatment of this infraspecific variation. In a continuing series of papers, Rivas-Martinez (1967, 1976, 1979) and Greuter (1981) recognize a number of subspecies of *J. montana*, whereas Tutin (1976) recognizes none.

The only complete revision of *Jasione* is that of Schmeja (1931) but his work has, with good reason, been laid aside and it is the earlier work of Pugsley (1921) which most clearly outlines the current understanding of British Isles *J. montana*. Pugsley (1921) distinguished five, rather ill-defined, varieties; these are a decumbent sand-dune taxon *J. montana* var. *litoralis* Fr., a gross cliff-top taxon *J. montana* var. *latifolia*, a dwarf cliff-top taxon *J. montana* var. *maritima* Bréb., a glabrous variant *J. montana* var. *laevis* Duby and a tall variant *J. montana* var. *major* Mert. & Koch. The major problems with these taxa are that Pugsley's own annotated specimens (**BM**) do not correspond with his descriptions and that they were described in the absence of information on phenotypic variation in *J. montana*. Additionally, continental workers have described many largely undistinguished taxa, which may or may not occur in the British Isles.

FIGURE 1. The location of populations sampled for morphological analysis.

VARIATION IN *J. MONTANA* WITHIN THE BRITISH ISLES

SAMPLING, SCORING, CHARACTER SELECTION AND PRELIMINARY ANALYSIS

A total of 59 populations from a wide geographical and ecological range were sampled during the summers of 1977 and 1978. Fig. 1 shows their general location; grid references are given in Parnell (1980).

At each site 25 flowering specimens were collected at random, pressed and taken back to the laboratory for measurement. At some localities, seeds from another 25 randomly selected individuals were collected. These were sown individually in potting compost in 10-cm flower-pots and grown to maturity in a cold frame. Representative specimens of the wild populations are deposited in **ABD** and/or **TCD**. No population of less than 100 individuals was sampled.

39 morphological measurements, including four derived ratios, were made on all Scottish populations. Of these 39 measurements, 20 proved redundant due either to high correlation with another measurement or lack of variation and it was found that the remaining 19 adequately described a plant's morphology. These are listed in Table 1 and some are illustrated in Fig. 2.

TABLE 1. CHARACTERS USED IN THE ANALYSIS OF BRITISH ISLES *JASIONE MONTANA*

1. Plant height, measured from the base of the leaf-rosette to the top of the plant
2. Plant width, the widest diameter of the leaf-rosette or the total spread of any decumbent stems
3. Leaf length, measured on the fourth leaf down from the top of the main peduncle, is taken along the midrib from the base
4. Leaf breadth (the maximum breadth of the same leaf used in 3)
5. The maximum diameter of the peduncle, taken from just under the involucral bracts (Fig. 2, No. 5)
6. The maximum diameter of the largest flowering head (Fig. 2, No. 6)
7. The maximum diameter of the involucre (Fig. 2, No. 7)
8. The maximum length of the outermost involucral bract, from the base to its widest point (Fig. 2, No. 8)
9. The maximum length of the pedicel (Fig. 2, No. 9)
10. The maximum length of the calyx (Fig. 2, No. 10)
11. The maximum width of the calyx-teeth (Fig. 2, No. 11)
12. The number of flowers in the terminal inflorescence
13. The number of flowering stems
14. The ratio of plant height to width
15. The ratio of leaf length to breadth
16. The ratio of involucre to inflorescence diameter
17. The hairiness of the hypanthium. Recorded as present or absent
18. The hairiness of the plant. Recorded on a 0–5 subjective scale with 0=No hairs, 1=very few scattered hairs, 2=sparsely hairy, 3=moderately hairy, 4=hairy, 5=very hairy
19. The habit of the plant. Recorded as either decumbent or upright

Three characters, numbers 2, 12 and 13 (Table 1) were found to be non-normally distributed. These data were normalized using either a square root or a Log_{10} transformation. The transformed values were used in all further calculations. Three other characters, numbers 17, 18 and 19, were not measured on a continuous scale and were therefore not used in the multivariate analysis.

The size and shape of the involucral bracts has been a commonly used diagnostic feature both of British varieties and continental subspecies of *J. montana* and also of other *Jasione* species. However, analysis indicated that involucral bracts showed considerable variation in size, shape, toothing and colour both within a single plant and also between plants within a single population. The bracts illustrated in Fig. 3 are all taken from the main inflorescence of four adjacent individuals from a single Irish population of *J. montana*. Small variations in bract characters are, therefore, unlikely to be of taxonomic importance though large differences in the outer involucral bracts, e.g. ovate vs lanceolate, may still be of use.

Preliminary analysis also showed that there was continuous variation in height and leaf dimensions between and within populations. Therefore plants formally distinguished as *J. montana* var. *major* Mert. & Koch (mostly on the basis of their large size (Pugsley 1921)) do not warrant recognition. Equally, dwarf plants formally distinguished as *J. montana* var. *maritima* Bréb. (Pugsley 1921) were mostly found to occur intermingled with plants of larger size. A single population (C10) consisting entirely of dwarf plants and only separable on size characteristics from *J. montana* var. *montana* was found. Continuous variation also occurred in the density of the indumentum between plants within a population, some being almost glabrous whilst others were hirsute.

NUMERICAL ANALYSIS OF POPULATIONS

The main numerical analysis was carried out on 1025 plants representing 41 of the 59 sampled populations. Additional analysis, using means of population characters, was carried out on the 32 populations of *J. montana* sensu stricto.

I used two fundamentally different multivariate techniques to analyse the data. The first, Principal Components Analysis (PCA), I used to examine patterns of variation or groupings of plants present in both meaned and raw data. Technically, PCA aims to produce axes which summarize the raw data and against which combinations of plants or other entities can be plotted. Its interpretation is often difficult because simple biaxial plots, which are the type most often used, are limited views of any variation pattern, and their interpretation depends on the percentage of the variance accounted for by each axis. The programme used was BMDP4M (Frane & Jennrich

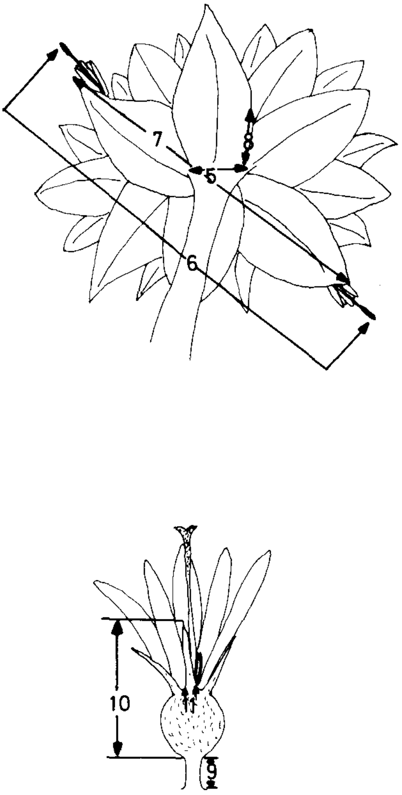

FIGURE 2. Morphological measurements made on the flowers and inflorescences of *J. montana*. The numbers refer to the corresponding characters described in Table 1.

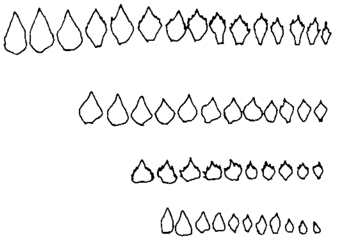

FIGURE 3. Bract outlines, from the outermost (left-hand) to the innermost (right-hand) bract, for four adjacent individuals from a single population of *J. montana* at Carnsore point, Ireland (GR 31/12.04).

1977). The second technique, Discriminant Analysis (DSC), was used to test whether groups of individuals assigned to different varieties of *J. montana* could be separated on the basis of a particular set of morphological characters. It was also used to determine if populations retained their distinctive characters (i.e. group membership) on cultivation. DSC allows any change in morphology to be reflected as a change in group membership. Technically DSC can, as Marriot (1974) states, be thought of as a multivariate extension of analysis of variance. The computer analysis used was published in the SPSS series (Nie *et al.* 1975).

In addition to the multivariate statistics used, mean values and confidence limits were calculated for each of the characters measured. These univariate statistics were used to quantify and express differences in the morphology of the groups seen on PCA and discriminated by DSC.

RESULTS OF PCA, BASED ON ANALYSIS OF INDIVIDUAL PLANTS

Altogether, 16 axes were required to explain fully all the variance in the sample. Marriot (1974) points out that axes with eigenvalues less than unity account for less of the variance than a single individual variable and do not therefore represent a condensation of the data and should not be plotted. In this analysis only four eigenvalues had values greater than unity and only three substantially so. Axes one, two and three accounted for 40%, 12% and 10% of the total variance respectively. Axes one and two are plotted in Fig. 4.

Membership of previously accepted groups is indicated on the PCA plot (Fig. 4). The groups are defined partly on groupings noted in the field and partly on the basis of previous descriptions. The groups used were:

1. *J. montana* var. *litoralis* Fr., defined on the basis of its decumbent habit, short stature (<20 cm), small lanceolate leaves (0.5–1×0.2 cm) with unthickened margins, and involucral bracts which are rhomboidal, acute or obtuse and sub-entire and which do not exceed the inflorescence;
2. *J. montana* var. *latifolia* Pugsley, of upright habit, 10–30 cm tall and distinguished by its large sub-spathulate leaves (1–2.5×0.4–0.9 cm) which often have thickened margins, and its involucral bracts which are broadly ovate, acute or obtuse with obscure teeth and which exceed the inflorescence;
3. *J. montana* var. *montana*, containing all other plants of *J. montana*.

In Fig. 4, those plants which showed maximum overlap between the varieties, thereby emphasising any overlap between groups, have been plotted. Despite this, it is evident that Fig. 4 offers at least moderate support for there being a separation between the varieties recognized.

RESULTS OF PCA, BASED ON ANALYSIS OF POPULATIONS OF *J. MONTANA* VAR. *MONTANA*

PCA of *J. montana* var. *montana* populations (Fig. 5) showed that there are morphological differences between populations of this variety from different parts of Britain. For example, plants from Scotland tend to have more flower stalks, smaller bracts and to be taller in relation to their basal spread than plants from the rest of the country. Some individual morphological characteristics also showed variation between different geographical regions, e.g. more than 55% of flowers of plants from Cornwall, Devon and Dorset had a glabrous hypanthium, decreasing to 38% from south Wales and only 18% of those from north Wales and southern Scotland. Such differences are relatively minor in comparison to those that exist between the different varieties of *J. montana* detailed above and seem to be largely eliminated on cultivation under standard environmental conditions, but they are evident in herbarium collections.

RESULTS OF DSC, BASED ON ANALYSIS OF INDIVIDUAL PLANTS

An objective measure of the separation between the groups recognized in the PCA of individual plants was obtained by discriminant analysis. Two significant discriminant axes were extracted. The first and second discriminant functions respectively accounted for 67% and 33% of the total variance, were highly significant ($\chi^2=1519$, $p<0.01$ and $\chi^2=569$, $p<0.01$) and therefore gave a good summary of group differences. The F-values obtained for differences between the groups were all highly significant at $p<0.01$ (i.e. between *J. montana* var. *montana* and *J. montana* var. *latifolia*, between *J. montana* var. *montana* and *J. montana* var. *litoralis*, and between *J. montana* var. *litoralis* and *J. montana* var. *latifolia*). Thus the groups tentatively identified on PCA are very different from each other.

Fig. 6 shows the mean values for each character, together with the 99.9% confidence limits for all characters measured for all three varieties. The most important difference between *J. montana* var. *latifolia* plants and those of the other two varieties lies in the possession of bracts which are significantly longer to their widest point (Fig. 6A), in the larger size of the inflorescence and diameter of the peduncle (Fig. 6B, 6C & 6D), in their taller, narrower growth-form (Fig. 6E, 6K & 6L) and generally larger dimensions throughout (Fig. 6F, 6G, 6H, 6I & 6J). Plants of *J. montana* var. *litoralis* differ from plants of the other two varieties in their greater breadth, which is almost equal to their height (Fig. 6E & 6L), and their smaller flowering heads (Fig. 6B & 6C).

Thus these multivariate analyses have supported the separation of British Isles *J. montana* into three varieties; *J. montana* var. *montana*, *J. montana* var. *litoralis* and *J. montana* var. *latifolia* and have shown that morphological differences exist between populations of *J. montana* s.s. from different areas of Britain.

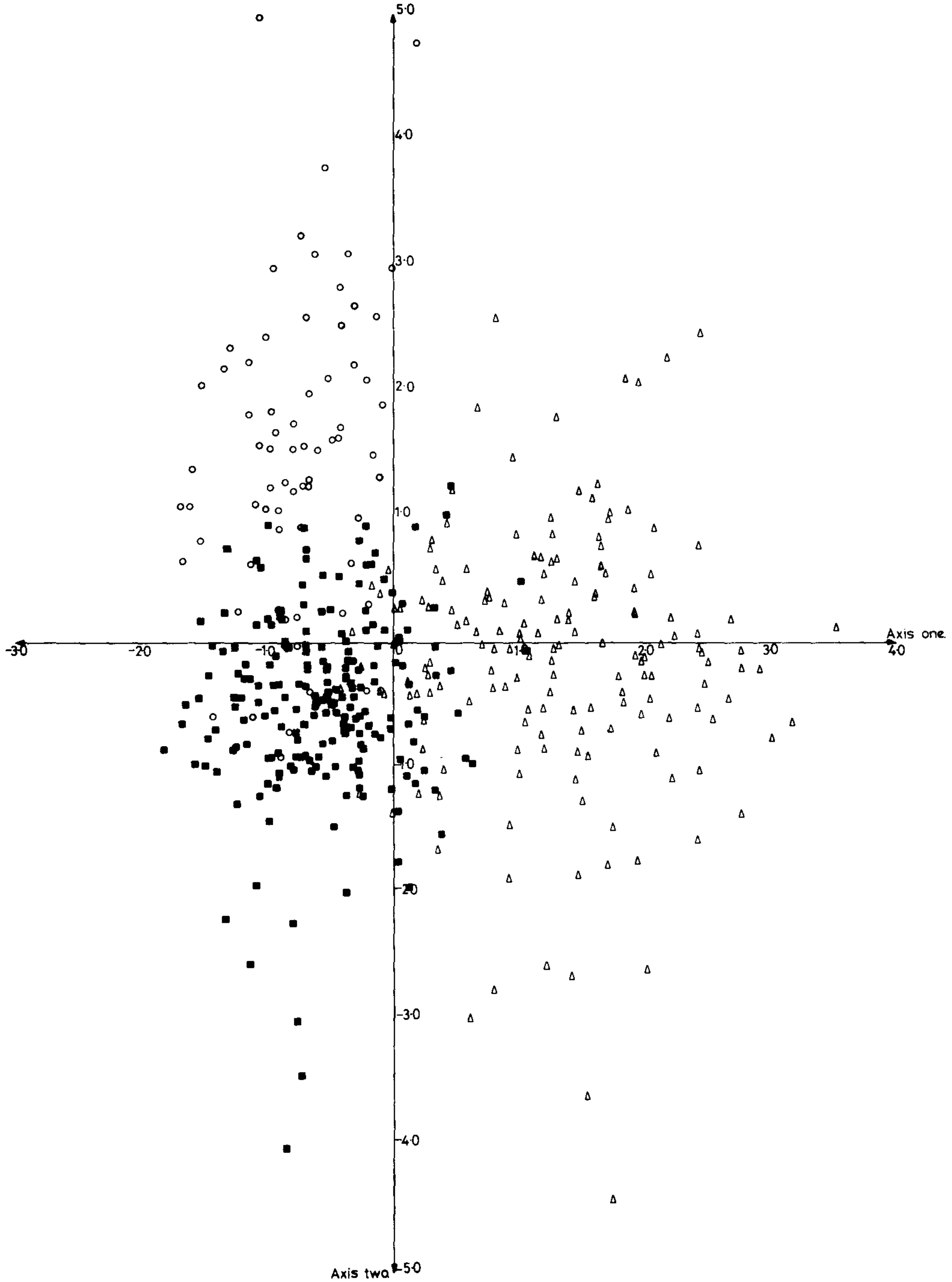

FIGURE 4. Principal components analysis on all plants sampled. The 500 plants giving the greatest degree of overlap are plotted. Axis One and Axis Two account for 40% and for 12% of the total variance respectively. ○=*J. montana* var. *litoralis*, △=*J. montana* var. *latifolia*, ■=*J. montana* var. *montana*.

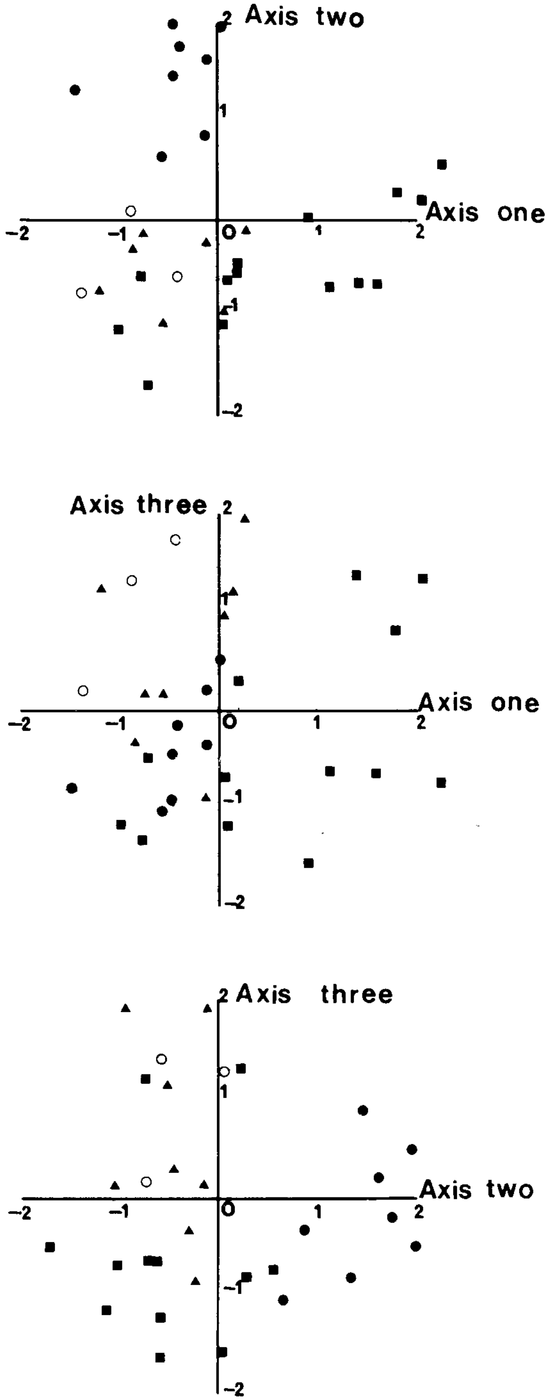

FIGURE 5. Principal components analysis of *J. montana* var. *montana* populations. Axes One, Two and Three account for 52%, 15% and 11% of the total variance respectively. ●=Scottish material, ○=Welsh material, ▲=Dorset material, ■=Cornish and Devon material.

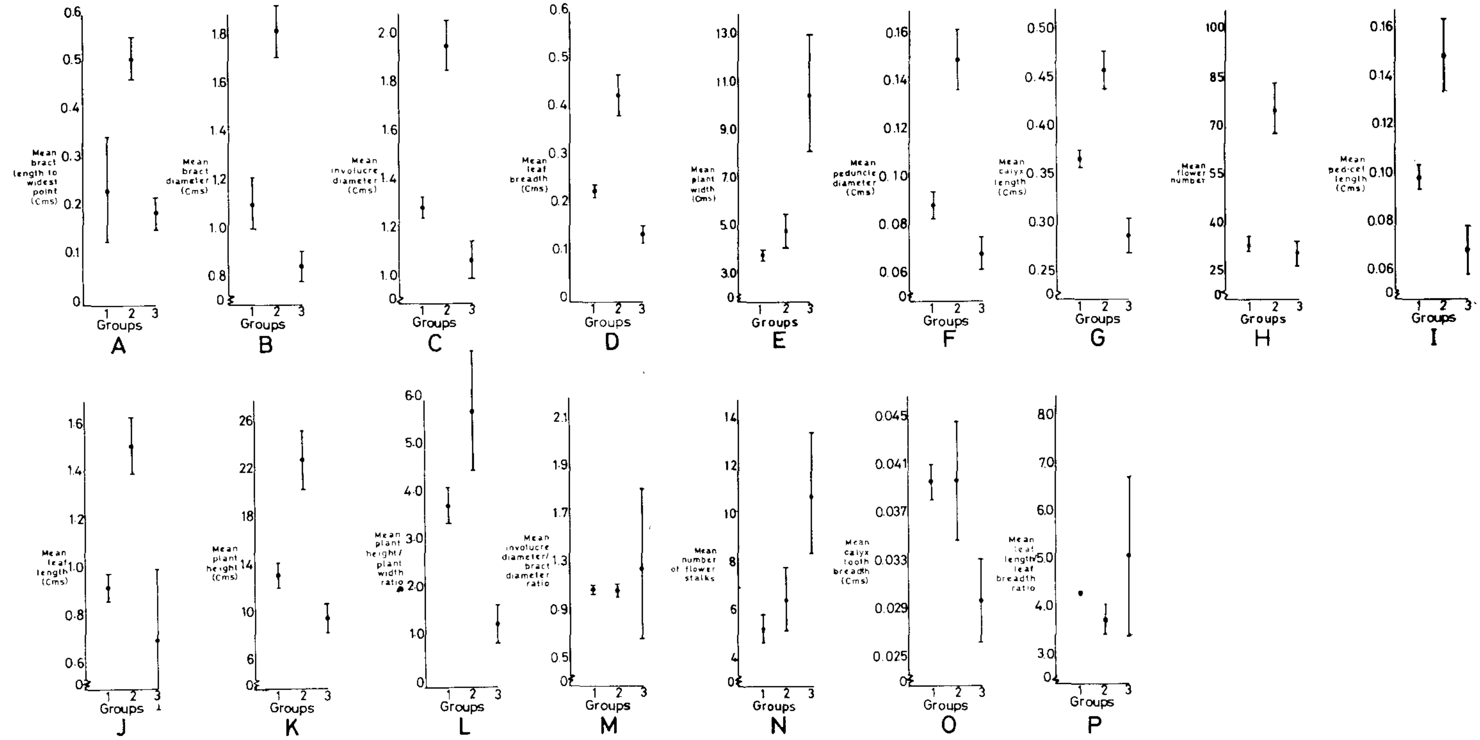

FIGURE 6. Mean values with 99.5% confidence limits for 16 characters measured in three groups. Group 1=*J. montana* var. *montana*, Group 2= *J. montana* var. *latifolia* and Group 3=*J. montana* var. *litoralis*.

STABILITY OF THE MORPHOLOGICAL GROUPINGS RECOGNIZED

A number of populations representing all the varieties of *J. montana* were grown under uniform environmental conditions. Plants were inspected and morphological measurements made on them at maturity. These measurements were plotted in the form of polygraphs and were also used in conjunction with the DSC functions already obtained from the wild populations (see above) to estimate the genetic component of the variation pattern of the varieties.

Representative polygraphs of the populations before and after cultivation are shown in Fig. 7. Wild populations are designated S16 (*J. montana* var. *montana*), I05 (*J. montana* var. *latifolia*), S05 and S14 (*J. montana* var. *litoralis*), and C10 (*J. montana* var. *maritima*). After cultivation under experimental conditions, the populations bear the prefix E, e.g. ES16.

J. montana var. *litoralis* populations (S05 &S14) vary in their response to cultivation (ES05 & ES14) (Fig. 7). ES05 plants maintain their diagnostic characteristics on cultivation, e.g. low height to width ratio but ES14 plants do not and come to resemble the experimental population of *J. montana* var. *montana* (ES16). Thus it seems that there are genetically determined plants assignable to *J. montana* var. *litoralis* but that there are also plants which, though similar in morphology, are in reality ecads or phenotypic copies of that taxon. This pattern of results was repeated in other tested populations of *J. montana* var. *litoralis*. Wild populations of *J. montana* var. *maritima* (C10) changed greatly on cultivation (EC10, Fig. 7) and came to resemble *J. montana* var. *montana* (ES16). *J. montana* var. *latifolia* (I05) remained distinct on cultivation (EI05, Fig. 7).

DSC analysis was used to test whether population means had shifted under cultivation, i.e. whether wild populations and the cultivated populations derived from them would be classified into the same group by DSC. DSC supported the conclusions drawn from the polygraphs by assigning all plants of EI05 to *J. montana* var. *latifolia*, ES05 to *J. montana* var. *litoralis* and ES16, ES14 & EC10 to *J. montana* var. *montana*.

Thus these experiments have shown firstly that plants grown from seed taken from natural populations of *J. montana* var. *litoralis* and *J. montana* var. *latifolia* maintain their distinctive morphologies on cultivation in uniform conditions and that the characteristics used to distinguish them are therefore genetically determined; secondly that phenotypic copies of *J. montana* var. *litoralis* exist and finally that plants of *J. montana* var. *maritima* do not maintain their dwarf stature on cultivation.

CROSSING EXPERIMENTS AND OBSERVATIONS ON POLLEN FERTILITY

Crossing experiments and observations on pollen fertility (Parnell 1980, 1982d, 1985) revealed no evidence of breeding barriers between or within any of the varieties. Artificial geitonogamous pollination, i.e. pollination between different flowers on the same inflorescence, produced a moderate amount of seed whereas strictly autogamous pollination did not. The distance seeds are likely to be dispersed in natural populations was likely to be less than 1.5 m, serving to restrict gene flow. Pollen infertility was variable both within an inflorescence and between different plants within a population and was also in some populations surprisingly high (c.36%), the infertility possibly acting as an insurance against excessive inbreeding (Parnell 1982d). So, despite the obvious physical adaptations of *J. montana* flowers to outcrossing (Knuth 1909; Parnell 1982d), successful inbreeding can and probably does occur at a fairly high frequency in natural populations.

THE VARIATION OF BRITISH ISLES MATERIAL

Experimental analysis has shown that it is possible to recognise taxonomically distinct, genetically determined, fully interfertile varieties of *J. montana* in the British Isles – *J. montana* var. *litoralis* and *J. montana* var. *latifolia*. The former is an ecotype confined to sand-dunes (Parnell 1980) whilst the latter grows on cliff-tops and roadside banks near the sea. Scattered populations of both occur throughout the British Isles. In general, Parnell (1982a) showed that *J. montana* is cytologically very uniform with $n=6$ or $2n=12$ but that *J. montana* var. *litoralis* is unique in the occasional possession of either one or two β chromosomes. Neither ecotype has a geographically circumscribed distribution and therefore neither warrants subspecific status.

Plants formerly recognized as *J. montana* var. *major* and *J. montana* var. *laevis* cannot be separated from *J. montana* var. *montana* and should not be maintained at varietal rank. Equally,

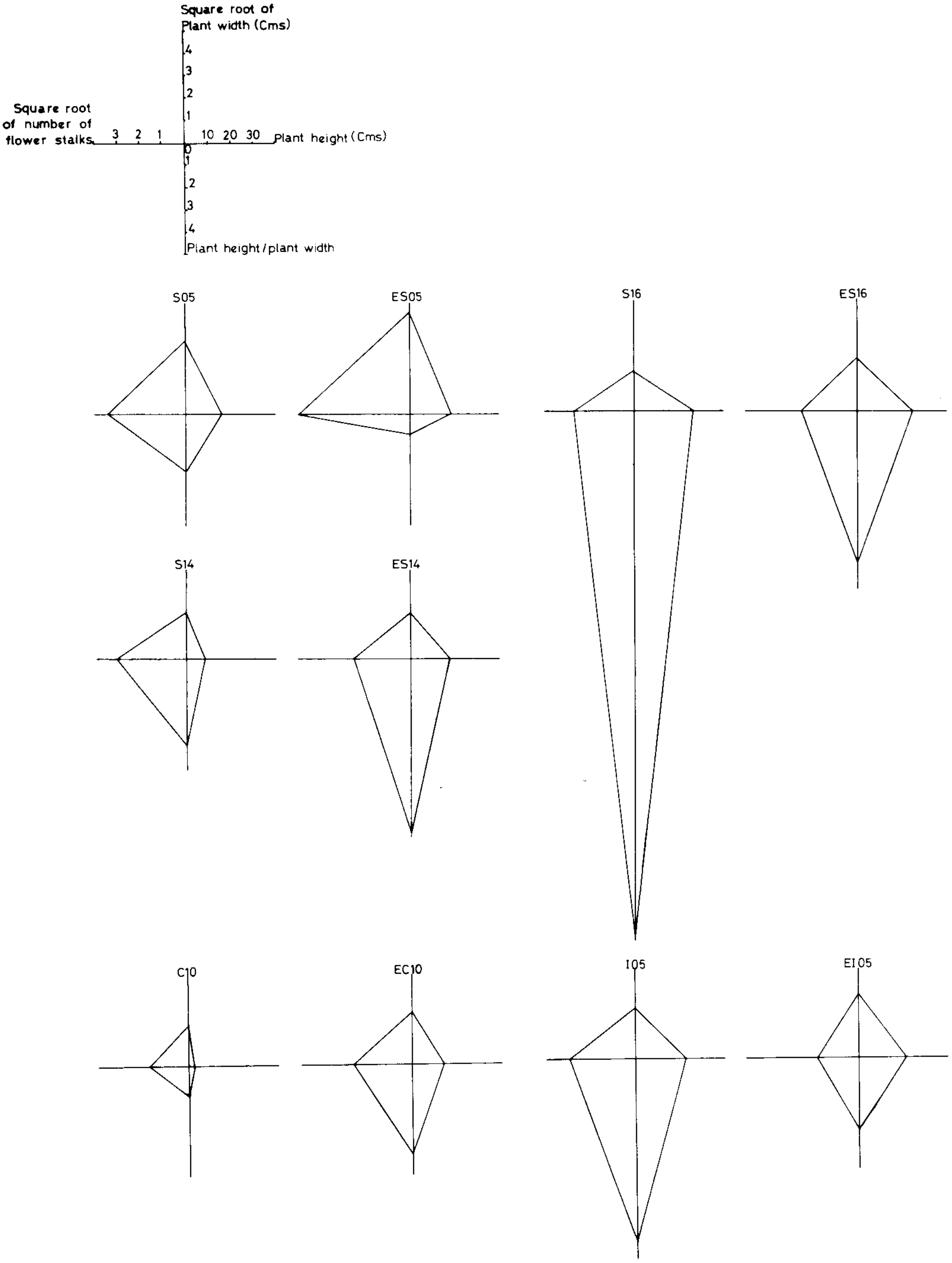

FIGURE 7. Polygraphs illustrating the morphological differences between and within populations of *J. montana* s.l. after growth under experimental conditions (prefixed by E) as compared with wild material. Wild populations are *J. montana* var. *montana* (S16), *J. montana* var. *latifolia* (I05), *J. montana* var. *litoralis* (S05 & S14) and *J. montana* var. *maritima* (C10).

plants of *J. montana* var. *maritima* fail to maintain their distinctive features on cultivation and therefore do not warrant recognition.

The geographical differences noted between northern and southern *J. montana* are small in comparison to the genotypical differences noted above and do not warrant formal taxonomic recognition.

The possibility that *J. montana* can act as an inbreeder has, surprisingly, not been suggested before. Undoubtedly geitonogamy must be of fairly common occurrence in any plant which bears more than a single flower and is not an obligate inbreeder. Why, in *J. montana*, such pollination should result in successful seed set whereas autogamous pollination does not is unknown. What is obvious though is that the morphology of *J. montana* belies its ability to self-fertilize. Such self-fertilization can be, at least to some degree, balanced by genetic recombination. As *J. montana* has a low chromosome number ($2n=12$) and rather small chromosomes with mostly few, terminal chiasmata (c. 1.4 per bivalent (Parnell 1982a)), it is clear that its chromosomal system is also acting to restrict rather than increase genetic variability. The occurrence of such physical and genetic inbreeding mechanisms allows successful recombinants to be conserved and together with restricted gene flow may allow the establishment of small morphological differences in plants from northern and southern Britain or northern and southern Europe.

VARIATION IN *J. MONTANA* THROUGHOUT THE REMAINDER OF ITS RANGE

CONTINENTAL MATERIAL

Analysis of herbarium specimens and natural plant populations of *J. montana* showed that the small morphological differences seen between *J. montana* from northern Scotland and south-western England (see above) were paralleled in material from continental Europe. For example, *J. montana* from southern Scandinavia is similar to Scottish material whereas that from central and southern Spain differs in its larger, often more deeply toothed bracts and pale green leaves. However, numerous intermediates connect northern and southern European specimens and there is no sharp discontinuity between them.

Spanish *J. montana* is very variable and two subspecies have been recognized, viz. *J. montana* subsp. *echinata* (Boiss. & Reuter) Rivas-Martinez and *J. montana* subsp. *blepharodon* (Boiss. & Reuter) Rivas-Martinez. The former subspecies is distinguished by its usually pale green, often hispid, leaves, purple, very deeply toothed and often strongly papillose outer involucral bracts and hispid calyx. However numerous intermediates between this and *J. montana* s.s. occur in Spain and also in Sicily, e.g. plants from the Sierra Marenna, near Cordoba (Spain), collected by Wilmott in **BM** have all of the above features except for the toothed purple bracts. The combination of characters defining *J. montana* subsp. *echinata* also breaks down because in the rest of the range of *J. montana*, e.g. in Britain, rare individuals occur which have the bract characteristics of *J. montana* subsp. *echinata* but none of the other features (*Parnell* in **ABD**). No chromosome counts are available for *J. montana* subsp. *echinata*. *J. montana* subsp. *blepharodon* is distinguished on the basis of its long (>2.7 mm), often basally ciliate calyx teeth, its generally sub-sessile flowers and large, ovate, more or less entire bracts. This combination of characters is unique. However, as both the number and position of the ciliate hairs on the calyx teeth is very variable (a situation similar to the variation in pubescence of the hypanthium of British *J. montana*) as is also the relative size and shape of the involucral bracts, it is clear that this combination of characters also breaks down. Finally, intermediates between these two subspecies also occur, e.g. *Reverchon 195* from Andalucia in **E** has ciliate calyx teeth and sub-sessile flowers but deeply toothed, purplish, strongly papillose outer involucral bracts. Bjorkqvist *et al.* (1969) showed that *J. montana* subsp. *blepharodon* had chromosomes which were numerically and morphologically identical with *J. montana* s.s.

Specimens of *J. montana* from the cliffs and dunes of the Atlantic coasts of Finisterre (Spain) and the Gironde (France) have often been distinguished as *J. montana* var. *sabularia* Cout. Typically, these decumbent plants (Fig. 8) bear short, imbricate, strigose leaves which have a markedly revolute margin. This combination of characters is unique and seems to occur only in specimens from coastal habitats in this region. Unfortunately the lectotype (in **BM**) and original description of this taxon (Coutinho 1913) neither correspond to the description given above nor in

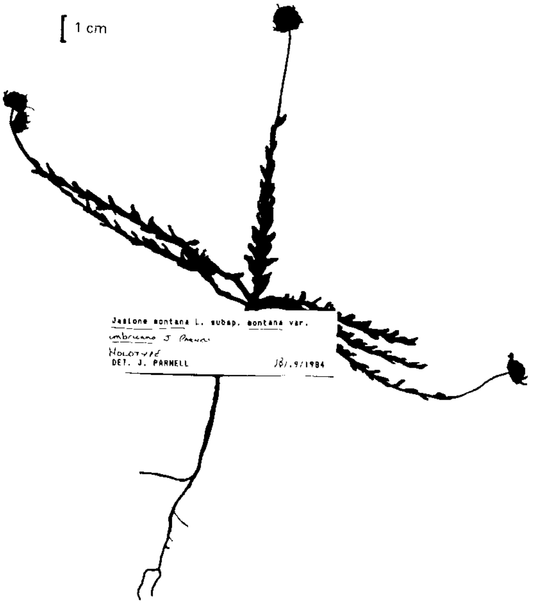

FIGURE 8. Holotype of *J. montana* L. subsp. *montana* var. *imbricans* J. Parnell. Finisterre, 1928, *Lacaita 32283* **(BM)**.

fact refer to a distinguishable taxon. Thus *J. montana* var. *sabularia* Cout. has been consistently misinterpreted. *J. montana* var. *sabularia* auct. non Cout. has the same habit as *J. montana* var. *litoralis* and is probably closely related to it.

Thus, though there is considerable morphological variation in continental European *J. montana*, the differences between specimens are often dependent on their distance apart with seemingly acute differences breaking down when plants from intermediate geographical localities are considered. *J. montana* var. *sabularia* Cout. is indistinguishable from *J. montana* s.s. However, *J. montana* var. *sabularia* auct. non Cout. is distinct, and bears a close relationship to *J. montana* var. *litoralis*.

NORTH AFRICAN MATERIAL

Jasione cornuta Ball is endemic to north-western Africa and differs from typical *J. montana* in its long, apiculate, large involucral bracts, relatively broad, papillose leaves (Fig. 9) and occasionally fimbriate calyx teeth. Some *J. cornuta* is different from any southern Spanish material notwithstanding an obviously close relationship between them. It would seem that the apiculate bracts and fimbriate calyx teeth of *J. cornuta* are a yet more extreme example of the great variation in bract and calyx characters that occurs throughout the range of *J. montana*, being especially noticeable in southern Spain and exemplified there by *J. montana* subsp. *blepharodon*. The broad, papillose leaves of *J. cornuta* also indicate a close relationship to *J. montana* subsp. *echinata* where these features occur in a less extreme form. Some specimens of *J. cornuta* are also obviously closely related to *J. corymbosa* Poiret and intermediates between the two species occur.

J. cornuta and southern Spanish *J. montana* share a number of morphological features. However the morphological differences between *J. cornuta* and *J. montana* s.l., combined with the geographical isolation of the former, mean that *J. cornuta* is best treated as a subspecies of *J. montana*, as suggested by Greuter (1981), though no reasons are given.

RELATED SPECIES

Both *J. corymbosa* Poiret ex Schultes and *J. penicillata* Boiss. have been treated as subspecies of *J. montana* by Greuter (1981) and Rivas Martinez (1976) respectively. *J. penicillata* is strongly

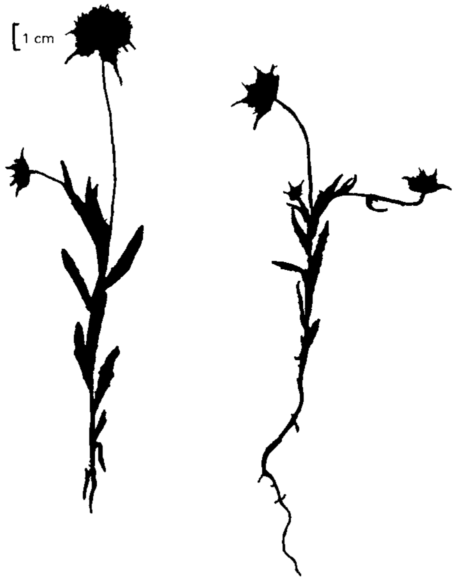

FIGURE 9. Plants of *J. montana* L. subsp. *cornuta* (Ball) Greuter & Burdet, collected from Morocco illustrating its long apiculate bracts and broad leaves. Morocco, 13/4/1969, *P. & J. Davis D 49337* (**E**).

pubescent, probably annual, endemic to the Sierra Tejeda and surrounding mountains and differs from all non-teratological *J. montana* in being usually unbranched, though the lectotype in **G** is highly branched, in bearing leaves all the way up the peduncle (Fig. 10), and in its linear-spathulate, apically villous calyx teeth. Its relatively isolated geographical location and unusual morphology indicate that it is best maintained at specific rank. *J. corymbosa* is typically a stout glabrous or hispid annual which is again leafy almost to the apex of the peduncle (Fig. 11), has subulate, villous calyx teeth and differs from all *J. montana* in usually bearing short, fastigiate inflorescence branches. It occurs in southern Spain and Morocco. Cytologically it is similar to *J. montana* s.s. with 2n=12 and has a similar karyotype (Parnell unpublished). In its common state it is so distinct from *J. montana* that it would seem best to retain it at specific rank.

J. heldreichii Boiss. & Orph. is morphologically similar to *J. montana*, differing largely in its lanceolate, aristate, very deeply toothed, involucral bracts. The bract shape and the degree of toothing are so different from that of *J. montana* that *J. heldreichii* plants are always easily distinguishable. Some plants of *J. heldreichii*, from north-western Turkey, can be separated from the rest because of their short, triangular calyx teeth and very strongly papillose and marginally thickened leaves and involucral bracts. Such plants only occur in the same region of northern Turkey as *J. heldreichii* s.s. and so only warrant varietal rank (Fig. 12). *J. heldreichii* has 2n=12 and a similar karyotype to *J. montana* s.s. (Contandriopoulos 1966).

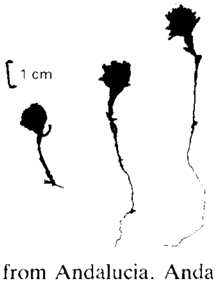

FIGURE 10. Plants of *J. penicillata* collected from Andalucia. Andalucia, 1889, *Reverchon 194* (**BM**).

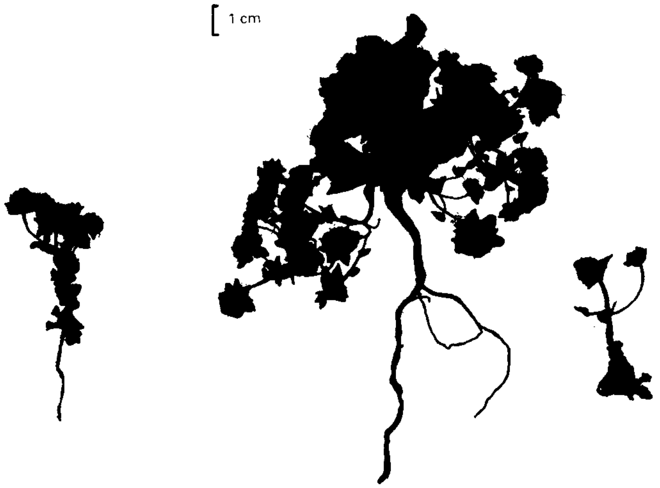

FIGURE 11. Plants of *J. corymbosa* collected from Morocco illustrating their generally fastigiate branching. Morocco, 29/6/1974 *Reading University/B.M. Exped. 1112* (**BM**).

FIGURE 12. Holotype of *J. heldreichii* Boiss. & Orph. in Boiss. var. *papillosa* J. Parnell. Istanbul, 8/8/72, *Uslu 2070* (**E**).

ENUMERATION OF TAXA

Only the synonyms of taxa recognized at the varietal level or above are cited. Sources for chromosome counts are given in Parnell (1982c) except where indicated.

1. *JASIONE MONTANA* L., *Sp.Pl.*, 928 (1753).
Jasione vulgaris Gaterau, *Descr. Pl. Montauban*, 153 (1789).
Jasione undulata Lam., *Encycl. Méth. Bot.*, 215 (1789), pro parte, excl. var. *ß*.
Jasione appressifolia Pau in *Not. Bot. Fl. Esp.*, **1**: 19 (1887).
Jasione espadanae Pau in *Not. Bot. Fl. Esp.*, **1**: 19 (1887).
Jasione adpressifolia Pau, orth. mut. ap. Willk., *Suppl. Prodr. Hisp.*, 126 (1893).
Jasione mediterranea Rouy, *Fl. Fr.*, **10**: 92 (1908).
Jasione hungarica Simonkai, nom. nud.

a. Subsp. *MONTANA*

i. Var. *MONTANA*
Jasione montana var. *ramosa* Latourette, *Chloris Ludgensis*, 25 (1785–1787), nom. nud.
Jasione montana var. *prolifera* Latourette, *Chloris Ludgensis*, 25 (1785–1787), nom. nud.
Jasione montana var. *major* Mert. & Koch in Röhling, *Deutschl. Fl.*, 147 (1826).
Jasione montana var. *laevis* Duby, *Bot. Gall.*, 311 (1828).
Jasione montana var. *hirsuta* Duby, *Bot. Gall.*, 311 (1828).
Jasione montana var. *prolifera* A.DC., *Monogr. Campan.*, 102 (1830).
Jasione montana var. *maritima* Bréb., *Fl. Normand.*, 179 (1835).
Jasione montana var. *glabra* Petermann, *Fl. Lips. Excurs.*, 168 (1838).
Jasione montana var. *stolonifera* DC., *Prodr.*, 415 (1839).
Jasione montana var. *gracilis* Lange, *Pug. Pl. Hisp.*, 155 (1861).
Jasione montana var. *genuina* Willk. in Willk. & Lange, *Prodr. Fl. Hisp.*, **1**: 126 (1870).
Jasione montana var. *gracilis* Timbal-Légrave in *Bull. Soc. Sci. Phys. Nat. Toulouse*, **3**: 419 (1875–1876).
Jasione montana var. *typica* Trautvetter in *Acta Horti Petrop.*, **6**: 44 (1879).
Jasione montana var. *hispida* G. Beck., *Fl. Nieder-Osterr.*, 1110 (1890).
Jasione montana var. *boraei* Rouy, *Fl. Fr.*, **10**: 91 (1908).
Jasione montana var. *timbali* Rouy, *Fl. Fr.*, **10**: 91 (1908).
Jasione montana var. *sabularia* Coutinho, *Fl. Port.*, 603 (1913).
Jasione pyrenaica var. *semiglabra* Sennen, *Plantes de Pyrenées-Orientales*, 5726 (1927), nom. nud.
Jasione montana var. *glaberrima* Podpěra in Polvíka, Domin & Podpěra, *Klíč k úplné květeně republiky C.S.R.*, 542 (1928).

More or less erect, sparingly branched (c. 2 flowering stems), usually villous biennials (rarely annual or short lived perennial) 2–60 cm tall. Stems usually leafless in their upper and leafy in their lower halves. Aerial leaves (0.9×0.2 cm) linear-oblong to lanceolate, always entire and often undulate (rarely crenate), the margin, unthickened, often weakly papillose and sometimes ciliate. Peduncles thin (<1 mm), outer involucral bracts, dark green, occasionally weakly papillose, ovate, parabolic, inner bracts, green or colourless, linear to lanceolate sometimes ovate, sometimes entire but more often crenate, serrate or laciniate, shorter than the flowers. Calyx teeth usually c. 2 mm long, subulate, green and often pubescent but never ciliate or fimbriate. Corolla usually blue, sometimes white or pink, <40 flowers in the primary inflorescence. Various abnormal forms of this variety occur and are described in Parnell (1982b, 1982c) and Scannell (1977). Distribution: throughout the range of the species excluding North Africa. n=6, 2n=12.

ii. Var. *ECHINATA* (Boiss. & Reuter) Willk. & Lange, *Prodr. Fl. Hisp.*, **2**: 282 (1870).
Jasione echinata Boiss. & Reuter, *Pugillus*, 73 (1852). Type: Gauchin, 1837, *Boissier* (Lectotype: G! fide Burdet, Charpin & Jacquemoud, in *Candollea*, **38**: 414). *Jasione montana* subsp. *echinata* (Boiss. & Reuter) Rivas-Martinez in *Publ. Inst. Biol. Appl. Barcelona*, **42**: 122 (1967).
Jasione montana var. *dentata* sensu Boissier, *Fl. Orient.*, **3**: 885 (1875) et auct.

Jasione montana var. *arenaria* Boiss. in sched.
Jasione stricta Pomel, *Nouv. Mat. Fl. Atl.*, 1 (1874).
Jasione montana var. *cartiliginea* Sennen, *Plantes d'Espagne*, No. 3461 (1918), nom. nud.

Plants are erect and sparingly branched 2–15 (−30) cm tall. Differs from var. *montana* in the usually pale green leaves, and pale green, often hispid, often generally purplish, long, thin, very deeply toothed and strongly papillose outer involucral bracts. Distribution: mainly in south-western Europe (Spain) but also in North Africa, Sicily, Italy and Corsica.

iii. Var. *BRACTEOSA* Willk. in *Bot. Zeit.*, **5**: 863 (1847).
Jasione blepharodon Boiss. & Reuter, *Pugillus*, 172 (1852). Type: Gibraltar, 1849, *Boiss. & Reuter* (Lectotype: **G**! fide Burdet, Charpin & Jacquemoud, in *Candollea*, **38**: 412 (1983)). *Jasione montana* subsp. *blepharodon* (Boiss. & Reuter) Rivas-Martinez in *Candollea*, **31**: 113 (1976); *Jasione corymbosa* Poiret ex Schultes in Roemer & Schultes var. *blepharodon* (Boiss. & Reuter) Batt., *Fl. Alger. Dicot.*, 571 (1889).
Jasione montana var. *littoralis* Boiss., *Voy. Bot. Midi. Esp.*, **2**: 396 (1839) non *J. montana* var. *litoralis* Fr., *Nov. Fl. Suec.*, 269 (1814). (I have been unable to find any specimens of this taxon and Burdet *et al.* (1983) have been unable to trace any in **G**. However, Boissier's original description and subsequent synonymy (Boissier & Reuter (1852)) makes this the most likely resting place for it.)
Jasione baetica Rodrig. in sched.

Differs from var. *montana* in being usually annual with papillose leaf-margins, ovate outer involucral bracts, mostly subsessile flowers and long (>2.7 mm), ciliate calyx-teeth. Distribution: mainly in south-western Europe (Spain). $2n=12$.

iv. Var. *LATIFOLIA* Pugsl. in *J. Bot., Lond.*, **59**: 215–216 (1921). Type: Bray Head, Co. Wicklow, 1881, *Britten & Nicholson* (Lectotype: **BM**!, designated here).
Jasione montana var. *megaphylla* Vicioso in *Anal. Jardin Botanico de Madrid*, **6**: 79 (1965).

Differs from var. *montana* in its lanceolate-spathulate leaves with thickened but not strongly papillose leaf-margins, thickened peduncles (c. 1.5 mm), large inflorescences with ovate involucral bracts projecting beyond the edge of the inflorescence and with usually >60 flowers in the main inflorescence. Distribution: scattered throughout Europe. $n=6$.

v. Var. *LITORALIS* Fr., *Nov. Fl. Suec.*, 269 (1814). Type: Halmstad par., Halmstad Holland, 1814, *E. Fries* (Lectotype: **UPS**! Lower specimen, designated here).
Jasione montana var. *littoralis* Koch, *Syn. Fl. Ger.*, 463 (1837).
Jasione montana var. *tenella* Petermann, *Fl. Lips. Excurs.*, 168 (1838).
Jasione montana var. *nana* Boreau, *Fl. Centre Fr.*, **2**: 286–287 (1840).
Jasione montana var. *nana* Gren. & Godron, *Fl. Fr.*, **2**: 398 (1850).

Differs from var. *montana* in having decumbent to ascending flowering stems. Plants are usually as tall as they are wide with >8 flowering stems and small (0.5–2 cm), narrow (c. 2 mm wide) leaves. Distribution: mainly on the coasts of Europe and Scandinavia (on sand) but also inland (on sand or granitic rocks). $n=6$ or $n=6+1\beta$ or $n=6+2\beta$.

vi. Var. **IMBRICANS** J. Parnell, **var. nov.**
Typus: Finisterre, 1928, *Lacaita 33283* (Holotypus: **BM**). Fig. 8.
Jasione montana var. *sabularia* auct. non Cout.

A varietate *montana* habitu decumbent et a varietate *montana* et varietate *litorali* caulibus floriferis paucis (1–3), foliis brevibus strigosis imbricatis marginibus saepissime revolutis, differt.

Differs from var. *montana* in its decumbent habit and from both var. *montana* and var. *litoralis* in its few (<4) flowering stems with short, imbricate, strigose leaves which usually have a strongly revolute margin. Distribution: coasts of Finisterre (Spain), Gironde (France).

b. Subsp. *CORNUTA* (Ball) Greuter & Burdet in *Willdenowia*, **11**: 40 (1981).
Jasione cornuta Ball in *J. Bot., Lond.*, **11**: 373 (1873). *Jasione corymbosa* subsp. *cornuta* (Ball) Murbeck in Jahandiez & Maire, *Cat. Pl. Maroc.*, 737 (1934).

Differs from subsp. *montana* in being usually annual with pale green leaves with strongly papillose margins, ovate, long acuminate outer involucral bracts, and linear/linear-spathulate aristate and often weakly fimbriate calyx teeth. Distribution: North Africa only.

2. *JASIONE PENICILLATA* Boiss., *Elenchus*, 63 (1838). Type: Sierra Tejeda, 1837, *Boiss.* (Lectotype: **G**! fide Burdet, Charpin & Jacquemoud in *Candollea*, **38**: 416 (1983)).
Jasione blepharodon subsp. *penicillata* (Boiss.) Rivas Goday in *Bol. Soc. Brot., ser. 2*, **47**: suppl. 168 (1973). *Jasione montana* subsp. *penicillata* (Boiss.) Rivas Martinez in *Candollea*, **31**: 113 (1976).

Differs from *J. montana* in being an annual or short-lived biennial 1–10 cm tall without a distinct leaf rosette but with lanceolate, entire aerial leaves 0.9 × 0.2 (−0.3) cm with a thin, neither undulate nor papillose margin and with the peduncle usually leafy up to the capitulum. Distribution: Sierra Tejeda and surrounding mountains, Spain.

3. *JASIONE CORYMBOSA* Poiret ex Schultes in Roemer & Schultes, *Syst. Veg.*, **5**: 474 (1819). Type: Tangier, 1794–1799, *Broussonet* (Lectotype: **M**!, designated here).
Jasione corymbosa Poiret in Lam., *Encycl. Méth. Bot. Suppl.*, **3**: 130 (1813), nom. prov.; *Jasione montana* subsp. *corymbosa* (Poiret) Greuter & Burdet in *Willdenowia*, **11**: 40 (1981) nom. illegit.

Differs from *J. montana* in being usually 3–10 (−15) cm tall, often fastigiately branched and with spathulate to ovate or obovate aerial leaves (6 × 2–4 mm) generally present up to the capitulum. 2n=12 (Parnell, unpublished). Distribution: southern Spain and Portugal and north-western Africa.

i. Var. *CORYMBOSA*.
As above and also usually villous.

ii. Var. **GLABRA** (Durieu ex Boiss. & Reuter) J. Parnell, **stat. et comb. nov.**
Jasione glabra Durieu ex Boiss. & Reuter, *Pug. Plant. Nov.*, 72 (1852). Type: Oran, 1840–1842, *Durieu* (Lectotype: **G**!, designated here). *Jasione corymbosa* subsp. *glabra* (Durieu ex Boiss. et Reuter) Batt. in Batt. et Trabut, *Flore de l'Algerie*, 570–571 (1888–1897).
Jasione arenaria Salzm. in sched.

Differs from var. *corymbosa* in being spindly and more or less glabrous with ovate involucral bracts. Confined to sand-dunes and connected by intermediates to *J. cornuta*.

4. *JASIONE HELDREICHII* Boiss. & Orph. in Boiss., *Diag. Pl. Nov.*, **3(6)**: 120 (1859). Type: Macedonia, 1857, *Orph.* (Lectotype: **G**!, designated here).
Jasione jankae Neilr., *Aufz. Ungarn. Slavon. Gefasspfl. Nachtrage und Verbesserungen*, 43–44 (1870).
Jasione glabra Vel. in *Ost. Bot. Z.*, **34**: 424–425 (1884).
Jasione heldreichii var. *microcephala* Vel., *Fl. Bulg.*, 374 (1891).

Differs from *J. montana* in having lanceolate, aristate, deeply toothed or cut/slashed involucral bracts. Biennial or perennial. Distribution: Balkan Peninsula and south-eastern Europe. 2n=12 (Contandriopoulos 1966).

i. Var. *HELDREICHII*

Jasione montana var. *dentata* DC., *Prodr.*, 415 (1839), non Boissier, *Fl. Orient.*, **3**: 885 (1875) et auct.

As above and with weakly papillose, slightly thickened leaf margins and green involucral bracts with long triangular calyx teeth.

ii. Var. **PAPILLOSA** J. Parnell, **var. nov.**
Typus: Istanbul, 1972, *Uslu 2070* (Holotypus: E!). Fig. 12.

A var. *heldreichii* foliis bracteisque involucri fortissime papillosis, marginibus conspicue incrassatis, bracteisque pagina interiore purpureis et dentibus calycis breviter (nec longe et anguste) triangularibus, differt.

Differs from var. *heldreichii* in its very strongly papillose and marginally thickened leaves, and involucral bracts which are also distinctly purple on their inner surface and in having short triangular calyx teeth. Distribution: north-western Turkey.

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