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A phenetic comparison of some *Fumaria* spp. (*Fumariaceae*)

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Key words: Angiosperms, *Fumariaceae, Papaveraceae, Fumaria.* – Phenetics, numerical taxonomy.

Abstract: The taxonomy of the genus *Fumaria* has not been considered in detail since Pugsley's work in 1919 ff., and few modern methods have been applied to it. In a phenetic study, 33 populations of 11 *Fumaria* spp. were grown in uniform conditions, and seven morphological characters measured. After re-expression and transformation the data were analysed by cluster analysis and principal components analysis. Alternative analyses did not indicate contradictory taxonomic conclusions. Artificial crosses gave some evidence on interfertility, and suggested *F. occidentalis* to be an allopolyploid of *F. bastardii* × *F. capreolata*. Pugsley's subsectional classification is supported within sect. *Parviflora*, but not within sect. *Grandiflora*. His two sections are seen to be meaningful, but not discrete.

Fumaria is a widespread genus of the *Fumariaceae/Papaveraceae*. Its members have some economic significance as weeds, and as sources of medical alkaloid drugs. The most recent sub-generic classification of *Fumaria* was that of Pugsley (1919, 1927, 1932, 1934, 1937) (Table 1). The present study applies phenetic methods to

Table 1. Pugsley's (1919, 1927, 1932, 1934, 1937) classification of *Fumaria*. Chromosome counts (2 n) from the literature are indicated. Only species included in this phenetic study or for which chromosome counts are available are included. "subsp.?" indicates that the original work did not indicate the subspecies involved

Sect. *Grandiflora*
  Subsect. *Agrariae*
    Ser. *Eu-Agrariae*
      F. agraria: 56 (Soler 1981), 80 (Queiros 1980), c. 80 (Björkqvist & al. 1969)
      F. occidentalis: c. 112 (Daker 1965)
      F. rupestris var *laxa:* 32 (Soler 1981)
      F. mirabilis: 64 (Lidén 1980)
      F. gaillardotii c. 96: (Soler 1981), 112 (Lidén 1980) [*F. bella*]: 80 (Lidén 1980)
    Ser. *Orientalis*
      F. judaica: 48 (Daker 1965)
      F. macrocarpa: 16 (Daker 1965)

Table 1 (continued)

Ser. *Anomales*
Subsect. *Capreolatae*
Ser. *Eu-Capreolatae*
F. capreolata
subsp.?: 64 (RYBERG 1960, DIERS 1961), c. 70 (SOLER 1981)
F. purpurea: c. 80 (DAKER 1965)
F. melillaica: 72–75 (LIDÉN 1980)
Ser. *Macrosepalae*
F. macrosepala: 32, 48 (SOLER 1981)
Subsect. *Murales*
Ser. *Eu-Murales*
F. martinii: 48 (DAKER 1965)
F. muralis
subsp.?: 48 (SOLER 1981, VAN LOON 1974)
subsp. *boraei:* 48 (DAKER 1965, QUEIROS 1980)
F. petteri subsp. *thurettii:* 32 (DAKER 1965)
Ser. *Sub-Agrariae*
F. bastardii: 48 (DAKER 1965, SOLER 1981), c. 48 (RYBERG 1960)
Ser. *Sub-Latisepalae*
F. reuteri: 48 (SOLER 1981)
Sect. *Parviflora*
Subsect. *Officinales*
F. officinalis
subsp.?: 16 (VAN LOON & VAN SETTEN 1982), 28 (SOLER 1981), 32 (RYBERG 1960, LÖVE & LÖVE 1956, MULLIGAN 1967, MÁJOVSKÝ & al. 1976)
subsp. *officinalis:* 32 (DAKER 1963, QUEIROS 1980, VAN LOON & al. 1971, MURIN 1976)
subsp. *wirtgenii:* 48 (DAKER 1965)
Subsect. *Latisepalae*
F. densiflora: 28 (SOLER 1981)
F. bracteosa: 16 (DAKER 1965)
F. rostellata: 14 (MURIN 1974, MÁJOVSKÝ & al. 1974)
F. faurei [*F. mirabilis*]: 80 (LIDÉN 1980), c. 84 (SOLER 1981)
Subsect. *Microsepalae*
Ser. *Ambiguae*
F. traubuti [*F. algeriensis*]: 40 (LIDÉN 1980)
Ser. *Eu-Microsepalae*
F. schleicheri: 32 (GVINIANIDZE & AVAZNELI 1982)
F. indica: 48 (BIR & SIDHU 1980)
F. vaillantii: 32 (RYBERG 1960)
F. parviflora: 32 (RYBERG 1960, KLIPHUIS & BARKOUDAH 1977, QUEIROS 1980, SOLER 1981), 48 (GUPTA & SRIVASTAVA 1971, VAN LOON 1974)

the study of relationships within the genus, based on 11 species grown in uniform conditions. Where possible, seed was obtained from several populations. This enables some examination of specific delimitation, judgement of species distinctions in the light of within-species variation, and a check on the methods used. However, practical constraints limited the total number of populations that could be handled.

Material and methods

Character measurement. Seeds were collected from wild populations of 11 species (Table 2), germinated, and the plants grown in uniform garden conditions at Aberystwyth, W. Wales. More than one population was sampled for four species, and for two subspecies of one of those. The populations were from Wales, England, and Germany. There were 33 populations in all. (All populations of *F. muralis* sampled were of subsp. *boraei*.) Preserved racemes and seed samples were deposited in the Herbarium of the University College of Wales.

Table 2. *Fumaria* spp. and populations sampled

Species	Population
F. occidentalis PUGSLEY	New Quay, Cornwall, England
F. purpurea PUGSLEY	Wollacombe, Devon, England
F. capreolata L.	New Quay, Dyfed, Wales Oxwich, West Glamorgan, Wales Woolacombe, Devon, England Bonn, Germany Leipzig, Germany
F. muralis SONDER ex KOCH	Aberystwyth, Dyfed, Wales (2 populations) Caldy, Dyfed, Wales Wollacombe, Devon, England (2 populations) Sidmouth, Devon, England Penryn, Cornwall, England Perranwell, Cornwall, England
F. martinii CLAVAUD	Penryn, Cornwall, England
F. bastardii BOREAU	Aberystwyth, Dyfed, Wales (2 populations)
F. officinalis L. subsp. *officinalis*	Aberystwyth, Dyfed, Wales Bromborough, Cheshire, England Hertford, Hertfordshire, England Barton Mills, Bedfordshire, England Ivinghoe, Buckinghamshire, England Harefield, Greater London, England Stanwell, Greater London, England Wollacombe, Devon, England Penryn, Cornwall, England
subsp. *wirtgenii* (KOCH) ARC.	Ivinghoe, Buckinghamshire, England Leipzig, Germany
F. bracteosa POMEL	Cyprus
F. densiflora DC.	Ivinghoe, Buckinghamshire, England
F. vaillantii LOISEL.	Ivinghoe, Buckinghamshire, England
F. parviflora LAM.	Ivinghoe, Buckinghamshire, England

It was intended to measure characters accurately on a reasonable number of plants. Practical limitations therefore dictated that only characters that were useful discriminants, and could be objectively quantified, be used. After preliminary investigation, these criteria led to the selection of the following characters, which were then measured on all plants:

Raceme length: racemes were taken from 10 plants per population in the middle of the flowering period, and 20 racemes measured per plant where available.

Number of flowers per raceme: sampled as for raceme length. Flowers that had matured into fruits and aborted flowers amongst fruits on the main rachis were counted, but not aborted flowers at the apex nor the occasional aborted flowers arising in the axils of other flowers.

Peduncle length: sampled as for raceme length.

Corolla length: 10 mature flowers were measured from each raceme.

Sepal length: sampled as for corolla length; defined as the distance from the apex to the point of attachment.

Sepal width (at the widest point): sampled as for corolla length.

Pollen grain diameter: Pollen was taken from four plants per population, from the oldest flower in each raceme not yet dehisced. 25 grains were measured per plant.

Character expression. The calculation of simple correlation coefficients between the seven morphological characters showed high collinearity (Fig. 1). Sepal width, sepal length, corolla length and peduncle length formed a highly inter-correlated group, all reflecting overall size. Most of these characters were therefore re-expressed:

Corolla length was included in the analysis as a simple measure.

Sepal length was re-expressed as:

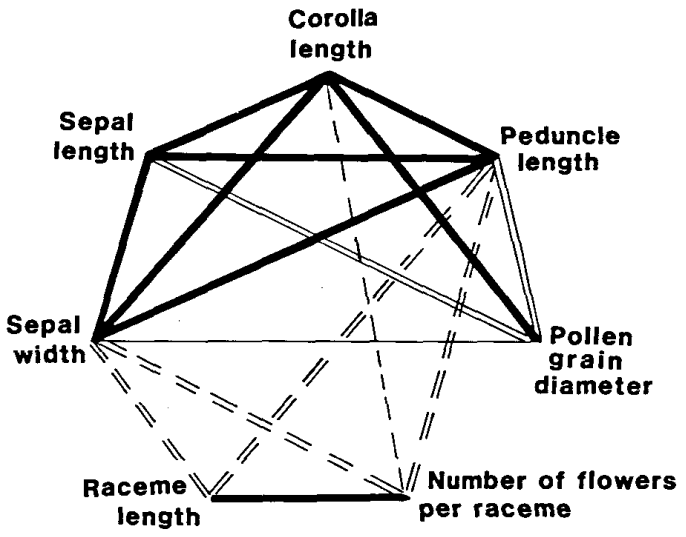
sepal : corolla length = sepal length/corolla length.

Sepal width was re-expressed:

sepal shape = sepal width/sepal length.

Peduncle length was re-expressed:

peduncle : corolla length = peduncle length/corolla length.



Key

R + ve, P<0.001

R + ve, 0.001 <P<0.01

R + ve, 0.01 <P<0.05

R − ve, 0.001< P < 0.01

R − ve, 0.01 <P < 0.05

Fig. 1. Significance of between-population correlation between the original variates

Pollen diameter was less highly correlated with this group; moreover whilst there is logical reason to expect the above group of characters to be intercorrelated, there is little a priori expectation (except perhaps via ploidy level) why pollen diameter should be correlated with them. Pollen diameter was therefore left as a simple measure.

Raceme length and the number of flowers per raceme were less strongly, and negatively, correlated with the characters discussed above. However, they were highly positively correlated with each other. Therefore:

Raceme length was left as a simple measure.

Number of flowers per raceme was re-expressed as:

flower spacing = raceme length/number of flower per raceme.

Variation in corolla and raceme length seemed likely, a priori, to be proportional to the mean, rather than additive; inspection of the distributions confirmed this. They were therefore log transformed. The distribution of ratios is intrinsically skewed; all ratios were therefore also log transformed. Since the units of measurement of length and of pollen diameter were arbitrary, all characters were standardized to zero mean and unit variance.

Analysis methods. Classification was performed by cluster analysis (SNEATH & SOKAL 1973), after re-expression, transformations and standardization as described above. Group average (=UPGMA) was the primary sorting strategy used, selected for its space conservation and lack of reversals (LANCE & WILLIAMS 1967). However, median (=weighted centroid) and nearest neighbour (=single linkage) sorting strategies were also used. The primary dissimilarity measure used was Euclidean distance (divided by the number of characters):

$$de_{jk} = \frac{1}{n}\sqrt{\sum_{i=1}^{n}(x_{ij} - x_{ik})^2}$$

where: de_{jk} = the Euclidean distance between OTU (operational taxonomic unit) j and OTU k, n = the number of characters, x_{ij} = the value of character i in OTU j, x_{ik} = the value of character i in OTU k.

Euclidean distance was selected as the primary measure of dissimilarity, because an Euclidean model seemed natural for log transformed and standardized data. However, city-block metric (divided by the number of characters) was also used:

$$dc_{jk} = \frac{1}{n}\sum_{i=1}^{n}|x_{ij} - x_{ik}|.$$

This is proportional to the Manhattan metric of LANCE & WILLIAMS (1967); it is the mean character difference of SNEATH & SOKAL (1973).

Principal components ordination was performed on the correlation coefficient matrix, after the same re-expression, transformation and standardization as above.

Interfertility. Artificial crosses were attempted between seven pairs of species/subspecies by hand pollination. Resulting seeds were germinated, and the growth of seedlings from them followed.

Results and interpretation

Populations within species. All subspecies and species represented by more than one population form discrete groups in the classification (Fig. 2). This supports traditional species delimitation in the genus. It is also support for the adequacy of using only seven characters, for the character transformation etc. and for the type of numerical classification used. Whilst perfect species discrimination could be

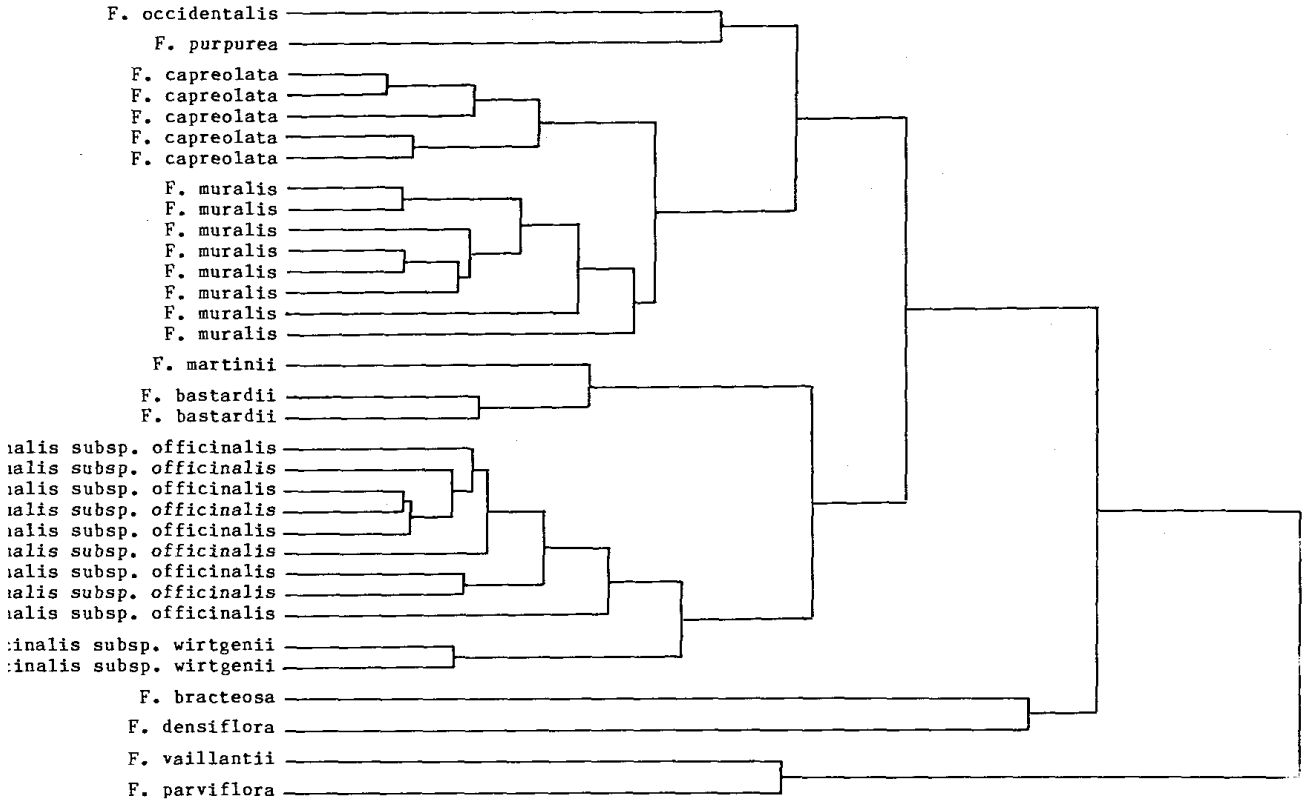


Fig. 2. Dendrogram from classification of the 33 *Fumaria* populations by cluster analysis, with group average sorting strategy and Euclidean dissimilarity

Table 3. Correlation coefficients between the PCA components and the variables in the *Fumaria* spp. investigated

Character	Component 1	Component 2
Corolla length	−0.893	+0.029
Sepal : corolla length	−0.647	+0.080
Sepal shape	+0.030	+0.809
Peduncle : corolla length	−0.836	+0.253
Pollen diameter	−0.717	−0.210
Raceme length	+0.052	−0.927
Flower spacing	+0.256	+0.631

coincidence, with inappropriate methods and indistinct species, it seems most likely that the methods a priori preferred supported the traditional species because those species are real and the methods are appropriate ones. ZAJAC (1974) also found that numerical classification distinguished between the two subspecies of *F. officinalis*, though with intermediates classified with both subspecies.

In the ordination too (Fig. 3, Table 3), the populations of any subspecies or species form a contiguous area. However, it is clear that there is considerable variation within some species, and the gaps between some species are quite small compared with this variation – for example between *F. capreolata* and *F. muralis*.

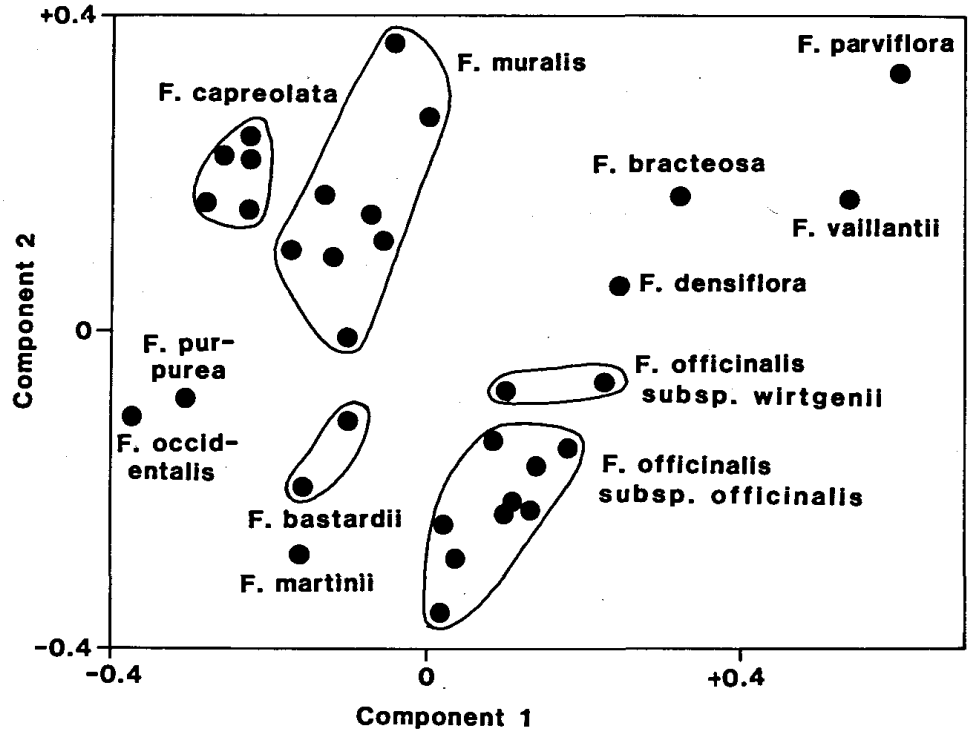


Fig. 3. Ordination of the 33 *Fumaria* populations by PCA, compared with PUGSLEY's (1919 etc.) classification

Species relationships. The phenetic classification is compared with PUGSLEY's (1919, etc.) classification in Fig. 4. There is considerable agreement, even allowing for rearrangement that has been made in PUGSLEY's order of taxa. Sections *Grandiflora* and *Parviflora* are supported to the extent that the representatives of subsectt. *Eu-Agrariae* and *Capreolatae*, and one representative of subsect. *Murales* form a group in the dendrogram. However, two other members of PUGSLEY's subsect. *Murales* of sect. *Grandiflora* fuse first with *F. officinalis* from the other section. The other two subsections of sect. *Parviflora* chain onto the other species, indicating that they are not particularly similar to each other.

The ordination (Fig. 3) confirms this. Although PUGSLEY's sections form two halves of the ordination diagram, there is no corresponding discontinuity. *F. officinalis* is indeed as close to *F. martinii* and *F. bastardii* of sect. *Grandiflora* as it is to *F. densiflora* and *F. bracteosa* of its own section. In terms of discontinuity, subsect. *Latisepalae* is indeed no closer to subsect. *Microsepalae* than it is to the remainder of the genus.

Subsections within sect. *Parviflora* are confirmed in that *F. vaillantii* and *F. parviflora* fuse first with each other (Fig. 4). *F. bracteosa* and *F. densiflora* also fuse first with each other, though at a high dissimilarity level, suggesting that from this evidence the subsection could be split.

Within sect. *Grandiflora*, PUGSLEY's subsections are not supported by this phenetic analysis. The two species representing subsect. *Capreolatae* fuse first with species in other subsections. The similarity across subsection boundaries between *F. capreolata* and *F. muralis* is seen also in the ordination (Fig. 3), where some populations of the two species approach each other closely. The dendrogram (Fig.

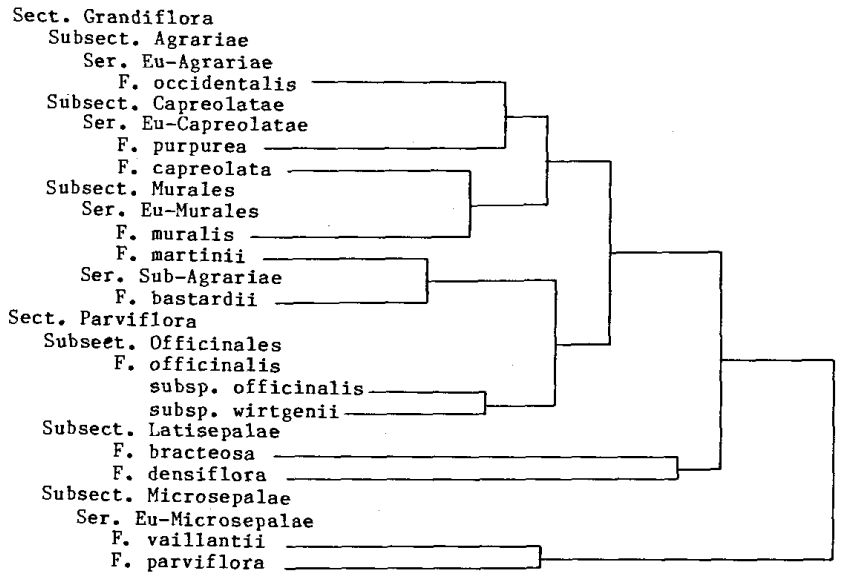


Fig. 4. Dendrogram from classification of the 33 *Fumaria* populations, truncated at the subspecies/species level and compared with PUGSLEY's (1919 etc.) classification. Only those taxa represented in the phenetic study are included

4) indicates them to be more closely related in the characters used than the two subspecies of *F. officinalis*. This supports HOOKER's (1884) treatment of *F. capreolata* and *F. muralis* as subspecies of one species.

Likewise, *F. occidentalis* and *F. purpurea* are shown by both the dendrogram (Fig. 2) and the ordination (Fig. 3) to be close, although PUGSLEY placed them in different subsections (Fig. 4). *F. martinii* and *F. bastardii* are indicated in the dendrogram as closer than some of the populations of *F. muralis* are to each other (Fig. 2), or some of those of *F. officinalis* subsp. *officinalis*.

Interfertility. There is a generally high degree of interfertility amongst these species (Table 4).

F 1 seedlings from the *F. muralis* × *F. martinii* cross were grown on, and they proved fully fertile, setting good seed. This supports PUGSLEY's classification, which placed them in the same series (Fig. 4) rather than our phenetic analysis, which placed them in rather separate groups.

Table 4. Results of artificial crosses between some *Fumaria* spp.

	No. of flowers	No. of mature fruit	Seed germination	Seedling development
F. muralis × *F. martinii*	15	11	+	+
F. muralis × *F. capreolata*	5	3	+	−
F. muralis × *F. bastardii*	5	4	+	+
F. muralis × *F. officinalis* subsp. *wirtgenii*	5	2	+	+
F. bastardii × *F. capreolata*	5	5	+	+
F. purpurea × *F. capreolata*	5	1	+	−
F. vaillantii × *F. officinalis* subsp. *officinalis*	5	4	+	+

The *F. bastardii* × *F. capreolata* F 1 seedlings were also grown on, but failed to produce good seed. Meiotic analysis of pollen mother cells from the hybrid showed some bivalent formation, together with numbers of univalents scattered throughout the cells. However, colchicine application to the stem apices of the F 1 plants produced some branches with the characters of *F. occidentalis*. Cytogenetic studies of mitotic chromosomes from apices of these branches, gave chromosome counts of approximately $2n = 112$, indicating a doubling-up of the hybrid component. Wild *F. occidentalis* also has a chromosome number of $2n = 112$, the sum of those of *F. bastardii* (48) and *F. capreolata* (64). The induced tetraploid branches set good seed. We suggest that *F. occidentalis* arose as a natural allopolyploid between *F. bastardii* and *F. capreolata*. Neither PUGSLEY's classification, nor our phenetic analysis, had predicted such an origin for it, both placing the putative parents and their offspring in rather different groups.

F. muralis × *F. officinalis* subsp. *wirtgenii* formed only two mature fruits, but the numbers are too small to draw conclusions. Anyway, both PUGSLEY and the present phenetic analysis indicate them as only distantly related.

F. muralis × *F. capreolata* failed to produce viable seedlings. This supports PUGSLEY, who placed them in different subsections, rather than the phenetic analysis, HAMMAR (1858) and HOOKER (1884), all of which classifications indicated them to be neighbours.

F. purpurea × *F. capreolata* also failed to produce viable seedlings. This supports the phenetic analysis, rather than PUGSLEY who put them in the same series.

Discussion

Robustness of the conclusions to analysis variants. JOHNSON (1970) points out that phenetic analyses can be subjective if the measure of dissimilarity or the sorting strategy are chosen subjectively. Here, character expression, transformation and standardization, as well as sorting strategy and dissimilarity measure were all chosen for a priori reasons (see Material and methods). Moreover, an independent test of the choice of methods is available from the treatment of populations of one species. The preferred method succeeded in forming pure groupings of the populations for all species and subspecies (Fig. 2). The results of alternative analyses (not presented) will be briefly described, to indicate the extent to which taxonomic conclusions would differ.

Using the city block metric in place of Euclidean distance, the dendrogram was almost identical; the only topographical difference was that one population of *F. muralis*, the last to join others of the species in our primary analysis, joined them after *F. capreolata*. This emphasizes the close similarity of those two species, and does not affect taxonomic conclusions.

Median sorting strategy is also space-conserving, and has the theoretical advantage over group average that it is less affected by a group of similar OTUs. However, it gave a dendrogram that was hard to use because of the presence of reversals, as is typical for this strategy (LANCE & WILLIAMS 1967). Differences from our primary analysis were minor. *F. purpurea* and *F. occidentalis* jointed the *F. capreolata*/*F. muralis*/*F. martinii*/*F. bastardii* group later and singly, and *F. vaillantii* and *F. parviflora* also joined singly.

Nearest-neighbour sorting, favoured by some numerical taxonomists (JARDINE & SIBSON 1968) gave, as usual (SOKAL & SNEATH 1973) considerable chaining. However, no contradictory taxonomic conclusions were indicated. For example, *F. officinalis* still joined first with species of PUGSLEY's sect. *Grandiflora*. There was still no support for PUGSLEY's sect. *Eu-Capreolatae* and ser. *Eu-Murales*; rather the affinity of *F. muralis* and *F. capreolata* was again emphasized.

Omitting all transformation resulted only in *F. purpurea* joining first with *F. capreolata*.

The ordination diagram (Fig. 3) indicates these variations as being alternative expressions of the relationships seen there, rather than as indicating different taxonomic conclusions.

We therefore believe our taxonomic conclusions from these analyses to be robust. Seven variates is a very small number, dictated largely by the paucity of differences between the species. However, our results suggest that seven variates, carefully measured and carefully analysed, can give meaningful results.

When multivariate methods such as these are used in ecology, they are used simply for data summary, and methods can be evaluated on the basis of their performance (e.g., WILLIAMS & al. 1973). In taxonomy, numerical methods should be a realization of the intended basis of taxonomy; there is little agreement on what that basis should be.

Evidence from cytology. *F. purpurea*, with a reported chromosome number of $2n=80$, would fit reasonably into subsect. *Agrariae*, as suggested by the dendrogram, since this number has been reported from subsect. *Agrariae* and not from other members of subsect. *Capreolatae* (Table 1). PUGSLEY's association of *F. muralis* and *F. martinii* is supported against the evidence of our analysis by their sharing a chromosome number of $2n=48$ (Table 1). However, the association of *F. bastardii* with *F. martinii*, suggested by the dendrogram, is supported by its having a diploid number of 48 also.

PUGSLEY's placement of *F. officinalis* in sect. *Parviflora* is supported by the commonest diploid chromosome number in *F. officinalis* being 32, and by this number being common in subsect. *Microsepalae* (Table 1). However, $2n=48$ is found in *F. officinalis* subsp. *wirtgenii*, and whilst this is also found in species and populations of subsect. *Microsepalae* it is the most common chromosome number in sect. *Grandiflorae*. No conclusion can be drawn in this case from the chromosome number.

Phenetics and biosystematics. We have suggested that *F. occidentalis* arose as a natural hybrid between *F. bastardii* and *F. capreolata*, yet our phenetic analysis separates the three, as does PUGSLEY's classification. There is no necessary conflict here. The infertility of the F 1 hybrid between them (without polyploidy) confirms that the putative parents are not closely related, in which case their hybrid could not be in the same grouping as both, and could well show similarities to a third grouping.

If a phenetic/biosystematic conflict is seen, it would be similar to that found by JACKSON & CROVELLO (1971) in *Haplopappus*, using many more characters (29 or 31), and by SMALL (1984) in *Medicago*. SMALL concluded that his phenetic analysis was more reliable than the similarity of a hybrid to a third species, but he did not have the confirmation from chromosome numbers that we have. JACKSON & CROVELLO (1971) suggested that such conflict was an estimation of the amount

of parallel evolution. Characters that have evolved in parallel can be valid evidence of relationship, since a tendency to evolve a character is evidence of genetic, epigenetic and hence phylogenetic affinity (CANTINO 1985).

Phytochemical evidence. The alkaloid parfumidine has been found in *F. officinalis, F. parviflora* and *F. vaillantii*, amongst other species (PREISNER & SHAMMA 1980), as have (−)stylopine and fumaritine (FORGACS & al. 1982). This could confirm PUGSLEY's placement, though it could be an artefact of the species that have been investigated, as evidenced by the more recent finding of fumaritine in *F. capreolata* (SENER 1985).

Conclusions

Although the classification (Fig. 2) and ordination (Fig. 3) are congruent with previous species boundaries, it must be noted that the dissimilarities between some species are smaller than those between others. *F. martinii* and *F. bastardii* fuse before all the populations of *F. muralis* and *F. officinalis* subsp. *officinalis*. *F. capreolata* and *F. muralis* fuse before the two subspecies of *F. officinalis*.

However, phenetic information on more characters would be required, with further information on incompatibility, before a definite conclusion could be made.

The present information supports PUGSLEY's subsectional classification within sect. *Parviflora*. Within sect. *Grandiflora* his subsections and series are suggested not to reflect the true relationships. *F. capreolata* and *F. muralis*, close in the present analysis, were placed in separate subsections by PUGSLEY, and in separate groups by HAUSSKNECHT (1873), though HAMMAR (1858) and HOOKER (1884) did show them as very close.

PUGSLEY's two sections are seen to be meaningful, but especially in the case of sect. *Parviflora* to represent in arbitrary division of continuous variation, especially in that *F. officinalis* is as close to members of the other section (Figs. 2 and 4). Close similarity between *F. parviflora* and *F. vaillantii*, and alignment at a higher level with *F. densiflora* and *F. officinalis*, are also seen in HAUSSKNECHT's (1873) classification, and HAMMAR's (1858) sections. Possibly, a desire to keep section sizes comparable affected the sectional delimitations of these authors.

We thank Dr G. L. RAPSON for assistance with the analyses.

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