

Isozymes, and the status of *Taraxacum* (Asteraceae) agamospecies

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HUGHES, L. & RICHARDS, A. J., 1989. **Isozymes and the status of *Taraxacum* (Asteraceae) agamospecies.** Genetic identities I and Similarity Indices SI are calculated between 12 samples of *Taraxacum*, on the basis of 40 isozymes at 15 loci for 10 enzyme systems. Samples included three polyploid agamosperous populations from northern England (group 1), three sexual diploid populations from south-central France (group 2), and six accessions of 'primitive' diploid self-compatible sexual taxa from southern Europe and Australia. Samples could be assigned to eight species, classified in seven sections of the genus.

Two clusters of high relationship were evident. All the group 1 and group 2 species were very closely related, with pairwise comparisons for I in excess of 0.93. The three group 3 accessions identified as *T. bessarabicum* showed pairwise comparisons for SI in excess of 0.71. Comparisons for SI between the other group 3 species, and between all the group 3 species and the group 1 and 2 species were all very low, not exceeding 0.45.

It is concluded that dissimilarity between samples as assessed by isozymes is probably related to the time of evolutionary divergence of those samples. Although allopolyploid, and morphologically very diverse, the group 1 agamospecies may have very recently diverged asexually from a common stock. The group 2 diploids may have resulted from rediploidization and regained sexuality from the same originally agamosperous stock. In areas of Europe in which such 'modern' sexuality is common, it is probable that all 'modern' *Taraxaca*, including at least five sections of the genus, should be included within a single taxon.

In contrast, 'primitive' self-compatible sexual species in group 3 appear to have diverged from each other several million years ago, and with the exception of the disjunct accessions of *T. bessarabicum*, are genetically highly distinct. Such species should be maintained in the taxonomies of all areas. It is probable that an agamospecies classification of 'modern' *Taraxacum* will continue to convey much useful information in areas, such as northern Europe, in which sexuality is absent.

ADDITIONAL KEY WORD: Agamospermy - Compositae.

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INTRODUCTION

Taraxacum (Asteraceae, Cichorieae), dandelion, forms a large, diverse, widespread and successful genus of rosette-forming, tap-rooted, ruderal

opportunists. Approximately 90% of taxa are polyploid (mostly $3x$, also $4x$, $5x$, $6x$ and $8x$), with an obligately agamospermous diplosporous parthenogenesis. The remaining 10% are sexual diploids ($2n = 16$) and are mostly fully self-incompatible (Richards, 1973, 1986).

Two contrasting philosophies have confused *Taraxacum* systematics for nearly 90 years, since the discovery of agamospermy in the genus by Murbeck (1904). In his monograph Handel-Mazzetti (1907) enumerates 57 species, each with a wide morphological scope. Some of these 'macrospecies' are employed today by non-specialists; more often the sections of the genus are used to convey wide-scope taxonomic information. Richards & Sell (1976) compromise, using agamospecies names to convey sectional or subsectional concepts within a binomial framework.

Since Dahlstedt (1905), many European and Asian (but not American) taxonomists have described *Taraxacum* species of a much lower morphological range or scope. As discussed by Richards (1973, 1985, 1986), these taxa, described as species, assume (usually covertly) an asexual breeding system, and it appears by implication, zero or minimal genetic variation. The nature of morphological variation within the genus is such that a very large number of useful taxa with distinctive behaviour and high homogeneity have been described; probably more than 2000 microspecies or agamospecies in all. Comparable situations are found in *Hieracium*, *Rubus*, and a few other agamic genera.

In *Taraxacum* the coexistence of taxa conceived using different philosophies but all recognized at the specific level has given rise to many problems. These can be summarized under three headings:

1. Most of the epithets of the macrospecies are untypified; by the standard of modern agamospecies taxonomy, they are of uncertain status, with uncertain boundaries, and tend to be ignored by specialists in the genus. However, if properly typified some macrospecies epithets might prove to be valid prior names for currently used agamospecies.

2. Specialists and non-specialists in the genus tend to use entirely different taxonomies. Thus, in the U.K., ecologists or physiologists still usually employ one of the four epithets listed in Clapham, Tutin & Warburg (1962); in contrast, *Taraxacum* taxonomists recognize over 250 agamospecies and classify these within ten sections of the genus. Only one epithet, *T. spectabile* Dahlst., is common to both classifications; used in the broad sense in the U.K. this epithet encompasses some 50 agamospecies placed in four sections of the genus.

3. The agamospecies philosophy has been found to be satisfactory, although complex and difficult for non-specialists to operate, within areas such as the U.K., Scandinavia and the Netherlands where sexuality is almost or completely absent. Tschermak-Woess (1949) and Frnkranz (1960) were the first to note that many *Taraxacum* species in central Europe are sexual diploids. Since then, comprehensive surveys by den Nijs & Sterk (1980, 1984a, b), Sterk, den Nijs & Kreune (1982), and J. Kirschner (personal communication) have shown that in France to the south of Paris, in southern Germany, lowland Switzerland, northern Italy and parts of Czechoslovakia and Austria, many populations of *Taraxacum* are entirely sexual or have both sexual and agamospermous individuals. Frnkranz (1966) showed that in populations with both sexuals and agamosperms, hybridization between the two types occurred, and this was

confirmed by Richards (1970b, c). Richards (1970a) and Müller (1972) showed that in such hybrid populations, triploid facultative agamosperms occurred, and more recently similar plants have been found by Jenniskens (1984).

When agamospecies specialists from northern Europe have attempted to apply narrow-concepts of taxa in areas of Europe with high proportions of sexual dandelions, they have found great difficulties (Richards, in the Auvergne, France; Kirschner in Czechoslovakia (personal communication); C. E. Sonck in France and Italy (personal communication)). In such populations, no two individuals show similar phenotypes, and only taxa of very wide scope perhaps at the level of the section or even wider than that, convey useful information. A similar argument holds for southern Japan, where diploid sexual *Taraxacum* predominate (Morita, 1976, 1980). Eight sexual species were originally described from this area by Kitamura (1957), but on the basis of taximetric studies, Morita (1985 and personal communication in 1986) suggests that only one variable species with three varieties should be maintained.

No clear ecological distinctions have emerged with respect to the distribution of sexual and agamospermous taxa. In Europe, it is certainly not possible to correlate sexuality in *Taraxacum* with latitude and climate. Recent studies in Greece (Richards, in press) enumerate 30 species (about ten more are also known), of which six are sexual and the remainder are agamospermous. Taxonomic confusion and hybridization rarely, if ever, occur in Greek *Taraxacum*, perhaps because sexual taxa rarely occur in the same populations as agamosperms. Sexual taxa occur from sea-level to 2600 m, but most are only distantly related to agamosperms, and may be considered as 'primitive' representatives (Richards, 1973). Such 'primitive' sexual taxa are also found further to the west, in Spain, France, Italy and Czechoslovakia. They tend to inhabit localities not favoured by other, agamospermous, *Taraxacum* such as Mediterranean (*T. serotinum* Poiret) or saline (*T. bessarabicum* (Hornem.) HM) habitats, and although morphologically variable, they do not hybridize with, and are not confused with, the more recently derived agamosperms.

This situation is quite different from that in central Europe where sexual taxa occur abundantly in the same derived sections of the genus (*Vulgaria* Dahlst., *Alpestris* van Soest, *Erythrosperma* (H. Lindb. fil.) Dahlst. and *Palustris* Dahlst.) as the agamosperms. Richards (1970a, c) and den Nijs & Sterk (1984) have found that morphologically indistinguishable individuals, assignable to a single agamospecies, can occur as sexual diploids and agamospermous triploids in central Europe. A discussion held under the auspices of the Netherlands Rijksinstituut voor Natuurbeheer at Terschelling, Netherlands in May 1986 recognized the problem that concepts of agamospecies break down in areas with a high proportion of diploid *Taraxacum* species, but no workable solution to the difficulty was arrived at.

Until now, studies on the taxonomy and classification of *Taraxacum* have relied on comparative morphology, and on cytology and karyology (e.g. Richards, 1973; Mogie & Richards, 1983). Hughes (1987) and Hughes & Richards (1985, 1988) have investigated the isozymes of 13 systems and more than 20 loci of various populations and accessions of *Taraxacum*. The primary aim of this study was to compare the genetic structure of related *Taraxacum* species with different breeding systems. However, the data also have important taxonomic implications with respect to the 'macrospecies' versus 'agamospecies'

problem, and with respect to the phylogeny of the genus, and these are discussed here.

MATERIAL AND METHODS

Full details of the experimental material are given in Hughes & Richards (1988). Plants investigated fall into three main groups which are briefly enumerated below:

1. Single populations of obligate agamosperms:

Taraxacum pseudohamatum Dahlst. *T.* section *Hamata* Ollgaard $2n = 24$. Newcastle upon Tyne. $N = 45$, (Code Ps).

T. unguilobum Dahlst. *T.* section *Celtica* Richards $2n = 32$. Hexham. $N = 30$. (Code Ung).

T. brachyglossum (Dahlst.) Dahlst. *T.* section *Erythrosperma* $2n = 24$. Seaton Carew, Durham. $N = 38$. (Code Br).

2. Single populations of self-incompatible sexual diploids, placed in *T.* section *Vulgaria*, but of uncertain specific identity, from the Auvergne, central France.

Code Au1 (originally from seed). $N = 28$ seedlings, from about 15 mothers.

Code Au2 (acquired as plants). $N = 75$.

Code PL (acquired as plants). $N = 43$.

3. Siblings from single capitula of 'primitive' sexual diploids of varied origin. In comparison with those under 2, all of these accessions proved to be fully self-fertile, apart from *T. serotinum*.

T. bessarabicum. *T.* section *Leptocephala* van Soest. St. Nectaire, France. Code SN.

T. bessarabicum. *T.* section *Leptocephala* van Soest. Zaragoza, Spain. Code Sal.

T. bessarabicum. *T.* section *Leptocephala* van Soest. Cluj, Romania. Code Bess.

T. serotinum. *T.* section *Serotina* van Soest. Macedonia, Greece. Code Ser.

T. pyropappum Boiss. & Reuter. *T.* section *Serotina* van Soest. Zaragoza, Spain. Code Pyr.

T. aristum Hagl. & Markl. *T.* section *Antarctica* HM. Victoria, Australia. Code Arst.

Each plant was tested for chromosome number and breeding system as described in Hughes & Richards (1988). Details of culture, sampling, extraction, and isozyme analysis are described in Hughes & Richards (1985, 1988) and in Hughes (1987).

RESULTS

For almost all the isozyme bands discovered in group 1 (obligate agamosperms) and group 2 (sexual plants, *Taraxacum* section *Vulgaria*), test crosses between different electrophoretic phenotypes were made, and polymorphic loci were shown to have electrophoretic bands of different mobilities which behaved in an allelic way with respect to each other (Hughes

& Richards, 1985, 1988). This was not true for esterase, and this system is not considered here. The genetic inheritance of isozyme bands found in group 3 ('primitive sexuals') was not tested, although genetically tested individuals in group 1 were run on the same gels as those in group 3, as controls. Many bands were found to have identical mobilities between group 1 and 3 and were assumed to represent the same allozymes.

As described in Hughes & Richards (1988), there was a remarkable correspondence between loci, allozymes and polymorphisms in the isozymes of plants in groups 1 and 2 (obligate agamosperms and sexual plants of *Taraxacum* section *Vulgaria*). Fifteen loci in ten isozyme systems were identified. Of these, eight loci were found to be monomorphic, or almost so, in both group 1 and group 2 populations. For group 2 populations, and for two of the group 1 populations, six loci were polymorphic, usually fixed heterozygously in the agamosperms. The third group 1 population, Br, was polymorphic at only four loci. The fifteenth locus was polymorphic at a low level in two of the group 2 populations, but was monomorphic in the other populations. One of the group 1 populations displayed an extra band, termed CAT a'. It is not known whether this was allelic to CAT a. Isozyme variation in group 1 and group 2 populations are summarized in Table 1.

In contrast, plants in group 3 showed less correspondence amongst themselves, and with plants in groups 1 and 2. No less than 14 new putative allozymes, not detected in groups 1 or 2, were found in these plants. None were thought to represent new loci, but new putative alleles were added to six loci thought to be monomorphic in groups 1 and 2. All the plants in group 3, with the exception of Ser., were fully self-fertile. In group 3 nearly all loci were homozygous within an individual, although it should be noted that each accession only involved seed from a single mother. However, for Ser., two of the 15 loci were heterozygous in at least some siblings. All homozygotes (i.e. all except Ser.) in group 3 showed invariable inheritance of isozymes, that is, offspring were identical to parents. This was also true for non-segregating triple-banded alleles GOT 2c and GOT 3c, which did not occur in plants in groups 1 and 2. Isozyme variation found in group 3 plants is also summarized in Table 1.

It is best if estimates of similarity between accessions are based on the variability inherent in most populations. With respect to plants in groups 1 and 2, more or less randomly sampled populations of sizes of between 28 and 75 individuals have been examined. For these six populations, two measures of genetic similarity have been used. The first of these is the normalized identity, I , defined by Nei (1975) as:

$$I = \frac{J_{xy}}{J_{xx} J_{yy}}$$

where J_{xx} , J_{yy} , and J_{xy} are the arithmetic means over all loci of $\sum x_i^2$, $\sum y_i^2$ and $\sum x_i y_i$, and x_i and y_i are allele frequencies at the i th locus in populations X and Y (Gottlieb, 1981). This statistic indicates the probability that a randomly chosen allele from each of two different populations will be identical, relative to the probability that two randomly chosen alleles from the same populations will be identical. Values of I vary from $I = 1$, where all allele frequencies in the two populations are equal, to $I = 0$, where two populations have no common alleles.

TABLE 1. Allele distribution in twelve populations and accessions of inbreeding, outbreeding and agamosperous *Taraxacum*.

		Ps	Ung	Br	Aul	Au2	PL	Sal	SN	Bess	Ser	Pyr	Arst.
MDH	a	+	+	+	+	+	+	+	+	+	+	+	-
	b	+	+	-	+	+	+	-	-	-	-	-	+
ME	a'	-	-	-	-	-	+	-	-	-	-	-	-
	a	+	+	+	+	+	+	-	-	-	-	+	-
	b	-	-	-	-	-	-	-	-	-	+	-	+
	c	-	-	-	-	-	-	+	+	+	-	-	-
IDH	a	+	+	+	+	+	+	+	+	+	+	-	+
	b	-	-	-	-	-	-	-	-	-	-	+	-
6PGDH-1	a	+	+	+	+	+	+	+	+	+	+	+	+
	b	-	-	-	-	+	+	-	-	-	-	-	-
6PGDH-2	a	+	+	+	+	+	+	+	-	+	+	+	-
	b	+	+	+	+	+	+	-	-	+	-	-	+
	c	+	-	-	+	+	-	-	+	-	-	-	-
GDH	a	+	+	+	+	+	+	-	-	-	+	+	-
	b	-	-	-	-	-	-	+	+	+	-	-	+
TYR	a	+	+	+	+	+	+	-	-	-	-	+	-
	b	+	+	-	+	+	+	-	-	-	+	-	+
	c	-	-	-	-	+	-	+	+	+	-	-	-
CAT	a'	+	-	-	-	-	-	-	-	-	-	-	-
	a	+	+	+	+	+	+	+	+	+	+	+	+
PER	a	+	+	+	+	+	+	-	-	-	-	-	-
	b	+	+	+	+	+	+	-	-	-	-	-	-
	c	-	-	-	-	-	-	+	+	+	+	-	+
	d	-	-	-	-	-	-	-	-	-	-	+	-
SOD-2	a	+	+	+	+	+	+	+	+	+	+	+	+
SOD-3	a	-	-	-	-	-	-	-	-	-	+	-	-
	b	+	+	+	+	+	+	+	+	+	-	+	+
GOT-1	a	+	+	+	+	+		-	-	-	+	-	+
	b	+	+	+	+	+		-	-	-	+	-	-
	c	-	-	-	-	-		-	-	-	-	+	-
	d	-	-	-	-	-		+	+	+	-	-	-
GOT-2	a	-	-	-	-	-	-	-	-	-	-	+	-
	b	+	+	+	+	+	+	-	-	-	-	-	-
	c	-	-	-	-	-	-	+	-	-	+	-	-
GOT-3	a	+	+	+	+	+	+	-	+	+	-	+	+
	b	-	-	-	-	-	-	+	-	-	+	-	-
ACPH	a	+	+	+	+	+	+	-	-	-	-	-	-
	b	+	+	+	+	+	+	+	+	+	+	-	-
	c	-	-	-	-	-	-	-	-	-	+	+	-
	d	-	-	-	-	-	-	-	-	-	-	-	+

The second measure of similarity is the standard genetic distance, D , defined by Nei (1975) as:

$$D = -\ln I$$

For this, D is an estimate of the accumulated number of electrophoretically detectable codon substitutions per locus since the time of divergence of the two populations. Values of D vary from $D = 0$, where there are no differences in allele frequencies between populations, to values of $D > 2.0$ where different genera have been compared (Hartl, 1980).

TABLE 2. Genetic distance and genetic identity for populations in groups 1 and 2.

		Aul	Au2	PL*	Ps	Ung	Br	
Group 2	{ Aul	—	0.99	0.99	0.96	0.99	0.98	I: genetic identity
	{ Au2	0.01	—	0.99	0.93	0.96	0.95	
	{ PL	0.01	0.01	—	0.94	0.98	0.99	
Group 1	{ Ps	0.04	0.07	0.06	—	0.95	0.93	D: genetic distance
	{ Ung	0.01	0.04	0.02	0.05	—	0.95	
	{ Br	0.02	0.05	0.01	0.07	0.05	—	

*Comparisons involving PL are based on fourteen loci.

For plants in groups 1 and 2, readings for I and D are given in Table 2. It is clear that these six populations are closely related to each other. It is of no surprise to learn that the three sexual populations from the Auvergne in group 2 are genetically very similar to each other, as assessed by the isozymes studied, with $I = 0.99$, and $D = 0.01$. However, none of the pairwise comparisons between group 1 and 2 populations drops below $I = 0.93$ or rises above $D = 0.07$, although comparisons include populations placed in four different sections of the genus, with diploid, triploid and tetraploid chromosome levels, with sexual and agamospermous breeding systems, and occurring up to 2000 km apart.

Plants in group 3 were obtained as seed samples from single mothers, rather than as population samples. Unfortunately, it is not possible to obtain estimates of either I or D for these samples in comparison with others, as those statistics depend on population data. Instead, Jaccard's Similarity Index (Jain & Singh, 1979) was applied. This measure is based upon the number of common categories, in this case isozymes, between the two groups.

$$SI = i / (n_1 + n_2 - i)$$

where n_1 and n_2 are the number of isozymes recorded in species 1 and 2 respectively, and i is the number of shared isozymes. SI has values ranging from $SI = 1.00$, where two species are identical, to $SI = 0$, where there are no common isozymes.

These values were computed pairwise for all samples in groups 1, 2 and 3 (Table 3). It should be noted that the nature of genetic variation within each sample, and the difference in the sampling between groups 1 and 2, and group 3, render the data used in these computations non-uniform in origin. Little within-population variation occurred in the agamosperm populations (group 1), in comparison with the variable sexual populations (group 2). However, as the agamosperms tended to be fixed heterozygotes for polymorphic loci, the mean number of alleles per locus did not differ statistically between the two groups (Hughes & Richards, 1988). This figure is much lower for the samples in group 3 taken individually (only 1.03 on average, compared to between 1.3 and 1.6 for populations in groups 1 and 2). No doubt, the low number of alleles per locus in group 3 is in part a function of the inbreeding system of these plants. The limited sampling of these plants (from single mothers) will also contribute

TABLE 3. SI pairwise comparisons between all 12 samples, from groups 1, 2 and 3.

	Aul	Au2	*PL	Ps	Ung	Br	Sal	SN	Bess	Ser	Pyr	Arst
Group 2	Aul	0.92	0.86	0.96	0.95	0.86	0.28	0.33	0.37	0.39	0.37	0.38
	Au2		0.87	0.88	0.87	0.79	0.30	0.36	0.39	0.37	0.34	0.36
	PL			0.83	0.90	0.81	0.30	0.31	0.40	0.33	0.40	0.36
Group 1	Ps				0.91	0.83	0.27	0.32	0.36	0.38	0.36	0.37
	Ung					0.90	0.29	0.30	0.38	0.41	0.38	0.40
	Br						0.31	0.32	0.42	0.38	0.42	0.32
Group 3	Sal							0.71	0.76	0.45	0.25	0.32
	SN								0.81	0.29	0.21	0.40
	Bess									0.33	0.30	0.35
	Ser										0.28	0.35
	Pyr											0.21

*Comparisons involving PL are based upon 14 loci.

greatly to the low allele diversity per sample. However, heterozygotes are very rare in these group 3 samples (frequency = 0.01, Hughes & Richards, 1988).

For the overall comparison of samples for SI (Table 3), two distinct groups of interrelated plants emerge. All the agamosperms in group 1 and the sexual populations from the Auvergne in group 2 are closely related to each other, as was also apparent from figures for I and D (Table 2). For readings of SI, the lowest pairwise comparison within these groups is 0.81 and the highest is 0.96. Comparable figures for I are 0.93 and 0.99 respectively. For SI, the asexual population Br shows the lowest mean resemblance in comparison with the other group 1 and 2 samples, while the sexual population Aul shows the highest overall resemblance. There is no indication of clear groupings within these six samples for SI, for instance between the group 2 sexuals, as was apparent in the populational comparisons computed by I.

The other interrelated group that emerges are the sexual inbreeders assigned to the species *T. bessarabicum*, codes Sal, SN and Bess. For this group, SI comparisons are from 0.71 to 0.81, comparable to some pairwise comparisons within the group 1 and group 2 cluster. This grouping is of interest in view of the widely disjunct distribution of this halophyte, and taxonomic arguments that have occurred over its status. Plants from the isolated French station at St. Nectaire (SN) have been called *T. salsugineum* Lamotte, and closely related species also occur in Turkey. *Taraxacum bessarabicum* also occurs in eastern Europe (Bess), and is recorded from South Africa, where it may or may not be native. The accession examined here from Spain (Sal) represents a new record for that country.

Outside these two groups, SI comparisons are low, varying between 0.21 and 0.45. The average of SI comparisons, except those between *T. bessarabicum* accessions, for the 'primitive' group 3 inbreeders is 0.31, while that between the group 3 inbreeders, including the *T. bessarabicum* accessions, and the 'modern' samples from groups 1 and 2 is 0.35. Overall, the Spanish accession of *T. bessarabicum* Sal shows the lowest resemblance to the group 1 and 2 samples, but it shows the highest resemblance to *T. serotinum*, although only at SI = 0.45. It is of interest that the geographically and taxonomically very remote species *T. aristum* (Arst), endemic to Australia, and related to species in New Zealand

and South America, should show SI comparisons with other samples comparable to the other, European, group 3 primitive sexual inbreeders. Another point of interest is that *T. serotinum*, and its Spanish relative *T. pyropappum*, which shows a close morphological resemblance to *T. serotinum*, and is placed in the same section, only show a very low SI comparison (0.28).

DISCUSSION

The close similarity between the isozymes of the British agamosperms (group 1) and the sexual outbreeders from the Auvergne, France (group 2) was unexpected. Apart from diagnostic bands at CAT for the agamospecies population Ps, at TYR in the sexual population Au2, and at ME for one individual in population PL, the isozyme profiles of individual agamosperms were indistinguishable from those of the group 2 sexuals. Most importantly, these six populations displayed gross morphological differences between themselves, which have led to their classification in no less than four different sections of the genus. In spite of these major differences, the populations shared the same few allozymes at almost every one of the 15 loci.

Equally striking, with the exception of resemblances between the three accessions of *T. bessarabicum*, Sal, SN and Bess, are the very low resemblances with respect to isozymes displayed between the sexual inbreeders, supposedly of a 'primitive' nature (Richards, 1973). This is despite the close morphological relationship between two of them, *T. serotinum* (Ser) and *T. pyropappum* (Pyr) in *T.* section *Serotina*, of which they are the only two members. These group 3 plants showed equally low resemblances to all the group 1 and group 2 populations. However, it should be strongly emphasized that such comparisons should be treated with considerable caution, as group 3 samples were taken from single capitula, and were not population samples.

Gottlieb (1977) in a survey of electrophoretic evidence from 28 plant species showed that the mean genetic identity (equivalent to normalized identity I in this paper) of conspecific populations was 0.95, and that of congeneric species was 0.67. More recent and larger surveys (Gottlieb, 1981; Crawford, 1983) gave similar values. On the basis of these comparisons, the genetic identities of the six populations in groups 1 and 2 of the present survey appear to fall within the conspecific category. The low values for SI for the group 3 species highlight the very high values for I and SI amongst the taxonomically unrelated taxa in groups 1 and 2.

However, Gottlieb shows that for annual inbreeders, different congeneric species may show values for I in excess of 0.90, in common with the values for I recorded here. Gottlieb suggests that perennials often evolve more gradually than annuals, and may consequently show smaller identities between species than annuals. The genetic identity of congeneric animal species that apparently originated in the Pleistocene are higher than those of more ancient species (Nevo *et al.*, 1974, Avise, Smith & Ayala, 1975). Many genetic differences between species may accumulate gradually after the genetic isolation of species; immediately after their origin, species may be limited genetic versions of their progenitors.

Richards (1973) originally suggested that derived allopolyploid agamospermous *Taraxacum* species originated during the Pleistocene when

'ancient' agamosperms, adapted to arctic conditions, came into contact with hybrid swarms of sexuals migrating northwards as the ice-sheets retreated. It is arguable that the high genetic identities and similarity indices recorded here between 'modern' (groups 1 and 2) taxa reflect this relatively recent divergence. However, more recently Mogie & Richards (1983) and Richards (1986) discuss evidence that at least some *Taraxacum* agamospecies appear to have diverged since their progenitor(s) evolved obligate agamospermy; that is that speciation took place asexually. This speciation might be post-glacial, or even more recent in origin. Also, it would occur from a series of very narrow genetic bases, indeed single genotypes. Such an explanation would certainly help to explain high genetic identities between taxonomically unrelated agamospermous polyploids (group 1) which, from both karyological (Richards, 1972, 1973) and electrophoretic (Hughes & Richards, 1988) evidence, appear to be allopolyploids.

Nevertheless, evidence from the taxonomically unrelated agamospecies *T. pseudohamatum*, *T. unguilobum* and *T. brachyglossum* suggests that they are too closely related electrophoretically for it to be likely that they had allopolyploid origins from genetically distinct diploid parents. It may be that the amount of asexual evolution in the genus is far greater than has hitherto been suspected. The close relationship of the 'modern' (group 2) sexuals suggests that these are also too closely related to the agamospermous polyploids to form only one of the genomes involved in the origin of the latter. Rather, these sexuals may result from rediploidization from facultatively agamospermous polyploid *Taraxacum*, of the kind described by Richards (1970, 1986) and Müller (1972). In this sense they are truly 'modern' (post-agamospermous) sexual diploids.

With the possible exception of *T. serotinum* (Ser), the group 3 'primitive' diploid sexuals are all fully self-compatible, and probably largely selfing in nature. The scarcity of heterozygous loci in these single accessions (Het = 0.001) supports this supposition. The low SI values obtained between selfing (group 3) accessions suggest that group 3 populations may have been separated geographically, and by their breeding system, for a sufficient period of time to allow considerable genetic differentiation. Van Soest (1958) and Fürnkranz (1969) suggested that the primitive diploid sexual species, with a fragmented distribution in the Mediterranean basin, from sections of the genus such as *Taraxacum* section *Leptocephala* (*T. bessarabicum*) and *T.* section *Serotina* (*T. serotinum* and *T. pyropappum*) are relicts from a Tertiary distribution around the ancient Tethys Sea and are therefore from 20M_a to 5M_a old.

It is difficult to assess the length of time that *T. aristum* has been isolated from other *Taraxacum* species in Australia. Richards (1973) has suggested that species in *T.* section *Antarctica* evolved from species in *T.* section *Arctica*, which occur in arctic America and elsewhere at high latitudes, having migrated down the American mountain chain. Whether these species then dispersed to Australasia before the final separation of the Gondwanaland mass (i.e. before 40M_a) or whether they have resulted from more recent long-distant dispersal is problematic. Either way, the date at which such populations dispersed southwards away from the Eurasiatic homeland of the genus, is likely to be placed well before the Pleistocene.

The present study suggests that the degree of differentiation of *Taraxacum* taxa, as assessed by isozymes, may largely be a function of the age of separation

of these taxa. The supposedly 'primitive' nature of such species at *T. bessarabicum*, *T. serotinum*, *T. pyropappum* and *T. aristum* is tentatively supported by their distant relationships to each other, and to 'modern' *Taraxacum*, although sampling is inadequate. The very close electrophoretic resemblance of taxonomically and chromosomally diverse 'modern' taxa suggests that they may have diverged very recently from a common agamospermous stock, and that 'modern' diploid sexuals may also have derived from this stock by rediploidization. This presents a very different picture of the evolution of *Taraxacum* agamospecies from that presented by Richards (1973).

A consensus is growing amongst specialists in *Taraxacum* taxonomy that in areas where sexuality is common, an agamospecies philosophy is not useful. The present study suggests that in such areas, all 'modern' *Taraxaca*, certainly those belonging to *T.* sections *Vulgaria*, *Alpestris*, *Erythrosperma*, *Celtica*, and *Hamata*, should perhaps be regarded as a single taxon. As discussed by Richards (1985), the commonly employed 'generalistic' epithets *T. officinale* Weber and *T. vulgare* Schrk. may not be available for this taxon. The first has been lectotypified as an agamospecies, and the second is confused and has not been typified. However, it is possible that these problems could be overcome by usage of '*sensu lato*'. In the absence of accurate typification, *T. vulgare* Schrk. *sensu lato* may convey the sense of the original author quite well when applied in the broad sense to 'modern' *Taraxacum* in areas where sexual populations are common. Equally, it is clear that certain 'primitive' diploid sexual taxa should persist at all taxonomic levels. Within the flora of Europe, these should certainly include *T. bessarabicum*, *T. serotinum* and *T. pyropappum* from the evidence of this study. It is probable that all species in the diploid sections *Glacialia* HM., *Orientalia* HM. *emend.* van Soest, *Rhodotricha* HM. *emend.* van Soest, and diploid species in *T.* section *Erythrocarpa* (e.g., *T. pieninicum* Pawl.), and *T.* section *Scariosa* (e.g., *T. minimum* (Brig.) Terracc.) should also be maintained.

No doubt, specialists will continue to use the agamospecies concept in areas of Europe in which sexual taxa are absent or rare. On present evidence these include Scandinavia, the Netherlands, Belgium, northern France and northern Germany, Poland, northern Czechoslovakia, the British Isles, USSR, the Alps and the Pyrenees above 1000 m, Iceland, Spain and Greece. Little is known about the distribution of sexual taxa and *Taraxacum* taxonomy in Hungary, Roumania, Bulgaria and Yugoslavia.

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