

## TARAXACUM: PLOIDY LEVELS, HYBRIDIZATION AND SPECIATION. THE ADVANTAGE AND CONSEQUENCE OF COMBINING REPRODUCTIVE SYSTEMS

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### Abstract

The genus *Taraxacum* comprises many hundreds of species, grouped into c. 40 sections. Approximately 21 sections are recorded from the Mediterranean area. Some are modern, derived (sections like *Ruderalia*, *Erythrosperma* and *Alpestris*), others primitive (among others, *Piesis*, *Glacialia* and *Rhodotricha*). The genus forms a polyploid complex with diploid up to octoploid representatives, triploids form the large majority. It was assumed that apomictic seed production prevailed in the large majority of the derived taxa, whereas sexual reproduction was said to be restricted to the primitive ones. Apomixis leads to fixed patterns of morphological traits within clonal families. The consequent, apparently consistent morphological differences between clones provided the basis for the extensive (micro-)taxonomy. However, sexual reproduction is more common than assumed: sexuality occurs in many sections. Ploidy level and breeding system are correlated: sexuality is strongly linked to diploids, and polyploids are usually apomictic. In the Mediterranean, diploid sexuals occur in 14 out of 21 sections. Purely diploid sections are the relatively primitive ones like *Piesis*, *Glacialia*, and *Oligantha*. In 10, possibly 11, more (species rich) sections, both sexual and asexual reproduction occur. In *Ruderalia* and *Erythrosperma*, co-occurrence of sexual diploids and asexual triploids in mixed populations is very common in central and southern Europe. The following has been found: 1, apomixis is not obligate, polyploids show a variable (low) degree of sexuality by means of several mechanisms; 2, in mixed populations, hybridization, and introgression between ploidy levels takes place; this also leads to 3), a di-/triploid cycle, that may bring extra potential for evolutionary response to environmental change. These processes may lead to: 1, the continuous production of new apomictic lineages (microspecies), 2, the fade-away of others (due to introgressive hybridization and selection), and 3, the generation of advanced diploids as well. It has been found that self-incompatibility of diploids may be broken down by pollen from polyploids. This gives diploid plants the possibility to reproduce in fully polyploid neighbourhoods, and favours the spread of diploids. Sections in which these phenomena are present, are to characterise as evolutionary very dynamic, but at the same time as taxonomically very difficult to treat, among other things, because the "micro-species" concept is of limited applicability. Given the presence of diploids and polyploids in many of the sections in the Mediterranean, this may well hold for some of these too.

### Introduction

Many taxonomists feel not particularly attracted to the genus *Taraxacum* Weber ex F.H.Wigg., to say the least. This is mainly because of the presence of a broad spectrum of morphological variation, that is reputedly organised in reproductively isolated

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\* This contribution is partly based on research carried out at the Institute for Systematics and Population Biology, and partly on two reviews on speciation processes in modern *Taraxacum* sections, viz., DEN NIJS & MENKEN (1994 and 1996). For that reason, the reader may well find some similarities between these.

apomictic clones; by consequence, the taxonomy since long is very complicated. The genus is widely spread all over the cool to warm temperate regions of the world. The centre of origin is traditionally postulated in central Asia (DOLL, 1982), where apart from derived ones, also many primitive taxa occur. Some of them have outpost locations around the mediterranean basin (STERK, 1987).

In apomictic organisms, genetic variation is organized among (reproductively isolated) clones, and therefore, the fixed morphological differences form the basis for an extensive micro-taxonomy. Also for that reason, *Taraxacum* is a large genus: approximately 2500 species have been described, in some 40 sections (RICHARDS, 1985, 1986; KIRSCHNER & STEPANEK, 1987, 1993, 1994). However, a revision would in all likelihood show that there are very many synonyms (OOSTERVELD, 1994). In this contribution, I will concentrate on other such questions as:

- 1, is apomixis obligate, and if not,
- 2, what are the consequences of partial sexuality, and finally,
- 3, does this affect taxa in the mediterranean region?

I will first give a short survey of our results from the section of the common Dandelions, *Ruderalia* Kirschner, H.Øllg. & Stepanek, and later discuss some of the consequences for the Mediterranean *Taraxacum* flora.

### **Polyploidy and Breeding system: Apomixis versus Sexual Reproduction**

The genus comprises a polyploid complex with the basic gametic number  $x=8$ . In nature, the majority of species are triploid ( $2n=24$ ), but plants up to the decaploid level can be encountered. Approximately 13% of the taxa are diploid, while the triploids and tetraploids comprise 52% and 28%, respectively (RICHARDS, 1973; DOLL, 1982). Only small amounts of higher ploidy levels are found. There is a correlation between ploidy level and breeding system: sexuality is strongly, though not exclusively, linked to diploids, whereas apomixis is only found in polyploids.

Most of the diploid sexual taxa are self-incompatible. Only species in a few sections (e.g. *Piesis* (DC.) A.J.Richards ex Kirschner & Stepanek), which are considered rather primitive (Doll 1982) are self-compatible. Recently, KIRSCHNER & al. (1994) found some tetraploids of the section *Piesis* in the Caucasus to be sexual. Studies by MENKEN & al. (1989) and MORITA & al. (1990a) have demonstrated the partial breakdown of the self-incompatibility system in the section *Ruderalia*. Pollen from triploids triggered diploid *Ruderalia* plants to successful self-fertilization.

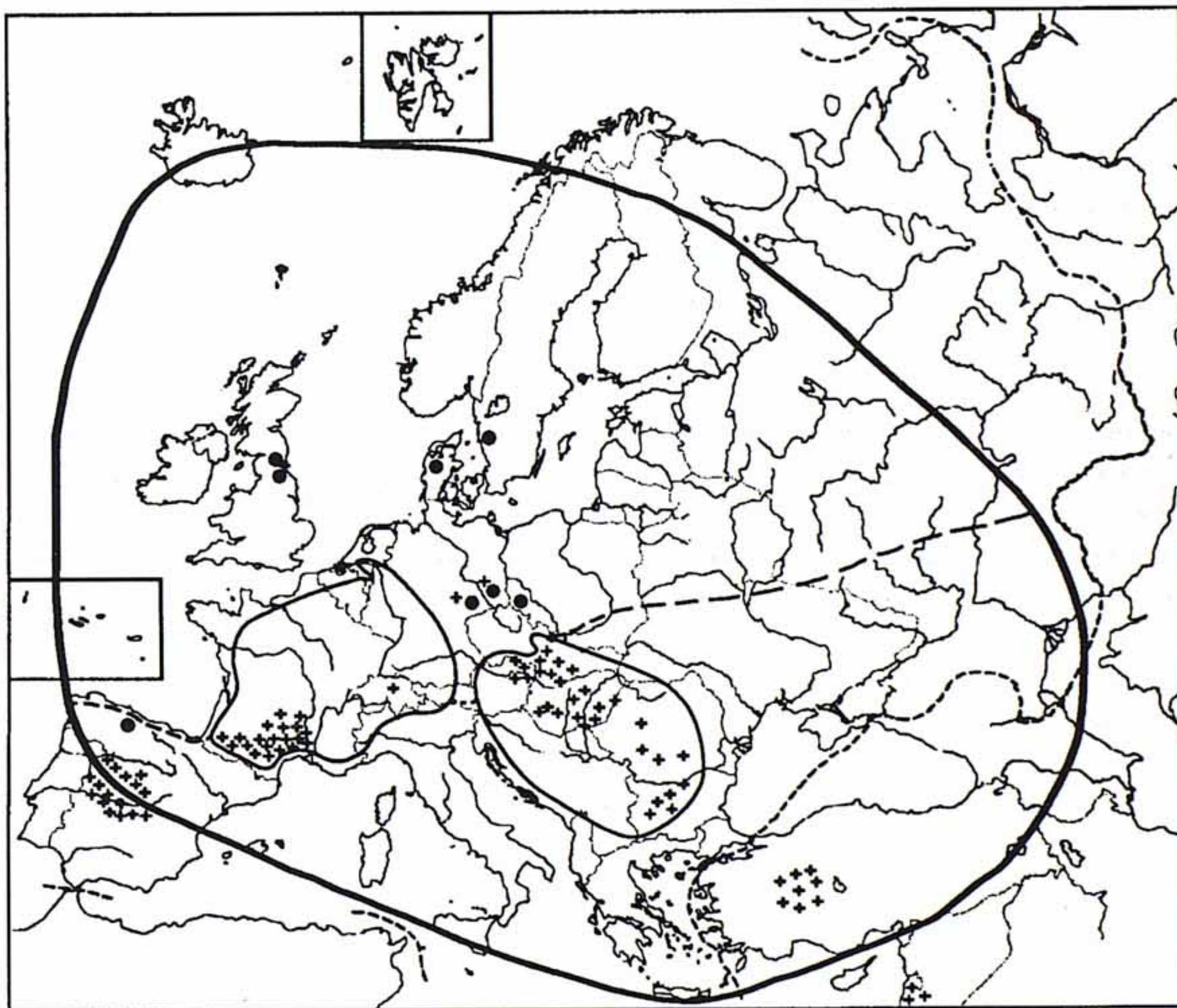
Very many of the microspecies have been based on the assumption of full apomictic behaviour and consecutive genetic isolation. However, it is well established now that sexual reproduction is less rare than commonly was assumed, and this may have consequences for taxonomy (KIRSCHNER & STEPANEK, 1994).

The strong correlation of ploidy level and reproduction mode gives us a clue for the analysis of the relative occurrence of both reproductive strategies. If we know the cytogeography, we also will know the distribution of sexuality and apomixis (den Nijs & Sterk, 1980).

### Cytogeography in a selected section: *Ruderalia*

In our group, we made a wide-ranging cytogeographic analysis based on the differences in pollen regularity between diploids (equally sized pollen) and triploids (strongly irregular pollen diameters), an approach originally published by TSCHERMAK-WOESS (1949). Chromosome counts in random subsamples confirmed the large majority of the pollen diagnoses.

The results of our cytogeographic studies are shown in Map 1 (DEN NIJS & STERK, 1980, 1984a & b; DEN NIJS & VAN DER HULST, 1988; DEN NIJS & al., 1990). For a more extensive list of references, see DEN NIJS & MENKEN, 1994, 1996). The supposedly natural distribution area of the section *Ruderalia* is indicated by the solid line in Map 1; nowadays, due to synanthropic dispersal, the section is almost cosmopolitan. Diploids of *Ruderalia* are common in the southwest and southeast of the



Map 1. Distribution of diploid representatives of the morphologically advanced sections *Ruderalia* and *Erythrosperma* in Europe (and part of the the Near East). The original distribution area of the section *Ruderalia* is indicated by the thicker line. Diploids of *Ruderalia* occur within the areas defined by the thinner lines, South of the dashed line these are supposed to occur. Black dots indicate isolated diploid sites. Diploid *Erythrosperma* locations are indicated by crosses (Further explanation in text). Adapted from den Nijs and Menken (1994), with permission.

original distribution area. Outside these areas, diploids of section *Ruderalia* are also expected to occur south of the dashed line, viz., on the Iberian peninsula and in South Ukraine. The disjunct distribution pattern is characteristic of post-glacial re-expansion from two amphialpine glacial refugia: one in the South(east) of France, and a second one somewhere in the Balcan area. Isolated diploid locations are found well North of the continuous areas. Triploids are almost everywhere, so most populations are mixed: diploids and triploids regularly grow together in the same field. Approaching the borders of the distribution area, diploids show a shift to relatively warm habitats, as has been demonstrated for The Netherlands (ROETMAN & al., 1988). The conclusion is that the sexual plants of the section prefer a relatively dry and warm climate. This explains the higher frequencies of these sexuals in the South of Europe.

One of the other conclusions that has been drawn from these data is that there are very many sexual plants co-occurring with the apomicts in the populations. This situation was hardly known by the taxonomists, who described hundreds of microspecies, assuming that all plants are equally fully apomictic.

Although the diploids that occur in some relatively primitive sections (examples: *Piesis*, *Oligantha* Soest, *Glacialia* Hand.-Mazz., *Rhodotricha* Hand.-Mazz.) are assumed to be relics, there is no evidence for this for the *Ruderalia*. Within this section, diploids are so similar to the morphologically advanced triploid plants, that DOLL (1982) concluded that those diploid plants must be advanced and of secondary origin instead of being relics from (pre-)pleistocene occurrence. Indeed, it is in many cases very difficult to distinguish diploid individuals from triploid ones on a morphological base. In several of our studies, we have reported tens of microspecies in herbaria comprising a mixture of triploids and diploids. Completely contrary to the assumption held by *Taraxacum* taxonomists, sometimes even the type material of a (micro-)species proved to be diploid. An example of these is the *Ruderalia* species *T. lawalreei* Soest (DEN NIJS & STERK, 1984a). DEN NIJS & VAN DER HULST (1988) assumed a similar situation for several taxa of section *Erythrosperma* (H.Lindb.) Dahlst., e.g., *T. brunneum* Soest, *T. marginellum* H.Lindb., and *T. rufulum* Soest.)

On the other hand, diploids may show in a single population a broad morphological spectrum of variation, where so called odd combinations of (originally triploid-apomictic) characters are represented in apparently such a blurred way that it confuses *Taraxacum* specialists. It has been proven that all diploids, irrespective of morphological differences between them, are fully interfertile, and cross readily (a.o. Jenniskens & al. 1984).

Given the facts that (1) sexuals and apomicts co-occur in many populations, and that (2) the morphological similarity between the cytootypes in many cases is so obvious, the question arises whether these two types of plants with their different reproductive strategies live completely separated or are to some extent in genetical contact, and possibly influence each other. Consequently, an important question to address is about apomixis in *Taraxacum*: is it complete, thus obligatory, or is there also partial sexuality in these plants?

### Is apomixis obligate?

The apomixis in *Taraxacum* is based on diplospory (ASKER & JERLING, 1992). This means that after the start of the first meiotic division some of the homologous chromosomes may form bivalents, but shortly after this, the process is disrupted and in stead of two daughter nuclei, a first division restitution cell is formed. Here, all chromosomes are united again in a single nucleus.

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#### Female function

chromosomal aberrations (hypotriploids)	SØRENSEN & GUDJONSSON (1946) SØRENSEN (1958)
reduced egg cells	FÜRNKRANZ (1961); MALECKA (1971)
reduced & fully unreduced egg cells	RICHARDS (1970a, b); MÜLLER (1972)
delayed gametophyte development	MALECKA (1965, 1973)

#### Male function

triploids fathering progeny of diploids	STERK (1987); MORITA & al. (1990b)
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#### introgression from male into female

allozyme analyses:

2x <i>Mongolica</i> > 3x <i>Ruderalia</i>	MORITA & al. (1990a)
2x <i>Ruderalia</i> > 3x <i>Ruderalia</i>	MENKEN & al. (1989, 1995)
2x <i>Mongolica</i> > 3x <i>Mongolica</i>	AKTER & al. (1991, 1993)

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Table 1. Mechanisms responsible for partial sexuality in apomictic *Taraxacum*.

In literature, we found many data indicating that partial sexuality in apomictic *Taraxacum* exists. From these studies also the conclusion can be drawn that this partial sexuality arises by several mechanisms, as is summarised in Table 1, taken from DEN NIJS & MENKEN (1996). For a more complete discussion of the processes involved in restoring (partial) sexuality in polyploids see Asker & Jerling (1992) and DEN NIJS & MENKEN (1994).

From the above the conclusion must be that:

- 1, due to several mechanisms, apomixis is far from obligate; and
- 2, polyploids may show a variable degree of facultativity in their apomixis;
- 3, there may, therefore, be a certain amount of gene flow between the cytotypes.
- 4, Consequently, there may be hybridogenous speciation.

### Hybridization: Indications for gene flow between ploidy levels

Using different molecular techniques several authors have recently studied possible hybridizations in *Taraxacum*. Based on r- and cp-DNA data, KING (1993) concluded that hybridization has repeatedly taken place between taxa of the common European and North American sections *Ruderalia*, *Erythrosperma*, *Hamata* H.Øllg. and *Celtica* A. J. RICHARDS.

In an allozyme analysis of a series of mixed diploid/triploid populations of *Ruderalia* from different regions in Europe, MENKEN & al. (1995) elucidated the genetic population structure. There is a remarkable resemblance between the gene pools of the diploid and the triploid population components. Allele frequencies showed quite an amount of homogeneity when ploidy levels were compared: in the majority of comparisons (18 out of 27 test cases) there was statistically significant similarity. Also testing for Hardy-Weinberg equilibrium in the 3x component revealed that in 19 out of 24 cases genotype frequencies fit H-W expectations. Apparently, the triploids form per population a near-panmictic community. Thus, allozyme data strongly suggest that there is much hybridisation going on in mixed populations, the individual plants forming a single mating community within at least some of the sites where ploidy levels co-occur.

STERK (1987) performed an experiment in which individual diploid *Ruderalia* plants were planted in a natural, fully triploid population in the northwestern part of The Netherlands, remote from the diploid distribution area. The diploids were isolated from each other so that diploid to diploid pollination was excluded. It appeared that pollination by triploid-born pollen resulted in a certain (beit low) amount of seed set (Table 2). The progenies raised from these seeds comprised sexual diploids as well as apomictic triploids and tetraploids, and also some aneuploid individuals. The new polyploid individuals most likely arose from different types of non-haploid pollen, having fertilized haploid ovules in the diploids. The study did not consider the possible development of non-reduced ovules in the diploids. Whether results like these are representative for the situation in nature is still a matter of debate. Recently, similar experiments were carried out in another Dutch mixed population, but contrastingly the

2x parents	Chromosomal composition of F1 plants					
	No. F1 plants	2x	aneuploids	3x	aneuploids	4x
S 13	22	13	2	4	3	–
S 15	23	6	2	9	–	6
S 16	19	4	1	10	1	3
Total	64	23	5	23	4	9
	36%	8%	36%	6%	14%	–
Reproductive mode	female: male:	sexual irregular, some sterile		apomict irregular		apomict irregular

Table 2. Ploidy levels and reproductive behaviour in progenies from free pollinated diploid mother plants, individually planted into 100% triploid populations near Abcoude (The Netherlands). All plants belong to *Taraxacum* section *Ruderalia*. After Sterk (1987), extended, with permission.

results show only a very small proportion of diploids (TAS & VAN DIJK, personal communication).

However, indications for a high level of hybridization between the ploidy levels also come from chromosome counts in a mixed population (Hedel, valley of the river Rhine, The Netherlands). In this study, a total of 82 plants were studied, 66 diploids and 16 triploids. Of the diploids, 45 showed some deviation of the euploid number by having one to three chromosomes extra, whereas 4 of the triploids show losses or gains of one to three chromosomes. Apparently, aneuploidy is fairly common, diploid individuals having supernumerary chromosomes, and triploids showing the gain or loss of one or more chromosomes (DIEFFENBACH & DEN NIJS, unpublished). Those aneuploid individuals strongly indicate the frequent occurrence of hybridizations between the ploidy levels. By being vital enough to reach the flowering stage in the local population, these plants also show a surprising fitness level.

The forming of new apomicts likely is a continuous process. A high number of clones in the mixed populations could therefore be expected. They were indeed found in the European study by MENKEN & al. (1995), and also in the Hedel population (calculated from DIEFFENBACH & DEN NIJS, unpublished). In 518 plants originating from a series of populations in the USA, LYMANN & ELLSTRAND (1984) found only 21 clones. A single 30 plant sample from a 2x/3x population in the South of The Netherlands, showed 16 clones, and a large sample of 262 plants from the Hedel population (see above) turned out to contain as many as 73 clones. The quite high figure for clonal diversity (0.94) suggests that almost every individual is a particular genotype (for details, see MENKEN & al. 1995; DEN NIJS & MENKEN, 1996). Altogether, there is ample data that point to the occurrence of bidirectional hybridizations between (at least some) polyploids and sexual diploids where these ploidy levels co-occur. This may mean that (1) progeny from diploids may contain hybrids that are fathered by pollen from polyploids, and, consequently, such progeny may comprise variable mixtures of hybridogenous di- and polyploids. On the other hand, (2) progeny from polyploids may be partly fathered by diploids, and therefore be also hybridogenous.

### **The di-/triploid Cycle and Climate Change, the Advantage**

The hybridizations mentioned in fact represent genetic exchanges between the ploidy levels within a population. These processes suggest strongly the existence of a diploid/triploid cycle in the section under study. The existence of diploid-polyploid cycles of development and evolution in several species complexes has been established. Well known examples are the *Panicum/Dichanthium* complex (de WET & HARLAN, 1970), and the genus *Potentilla* (ASKER, 1977; 1979). Considering all phenomena that lead to genetic exchange and hybridizations in *Ruderalia*, we conclude that also in this taxon a di-/triploid cycle exists in the regions of cytotype co-occurrence. In response to changes in the environment, the population complex of the *Ruderalia* is able to take profit of both reproductive systems. It therefore will have the advantages of both reproductive systems. In pioneer habitats, the almost 100% reproductive output, which is inherently independent of pollination, guarantees the triploids a successful population

development. On the other hand, there can be a shift to sexual reproduction in circumstances that favour genetic diversity. Currently, relatively warm and stable grassland vegetations in the southern half of Europe seem to fulfill these latter requirements. Given the trend of climatic warming, it may be expected that the distribution area of the diploids will extend to the North.

### **Consequences for Taxonomy**

As a consequence of the interplay between the breeding systems, the applicability of the "micro-"species concept is rather limited in regions of co-occurrence of di- and triploids. In general, there seems to be a shared gene pool in the mixed diploid-triploid area of distribution. There, formation of new apomictic forms and new diploids takes place, commonly by hybridization. Some of the new apomicts may establish and increase their distribution area, while, others will go extinct by selection or drift. The conclusion must be that it is very likely that in each population where diploids and triploids co-occur (-formally spoken-) new microspecies are formed. Of course, a large part of these will be insufficiently fit and never establish, but some may survive selection and add to the array of morphs in the pertaining population. As a consequence, the description at the species level of all discontinuities in the spectrum of apomictic morphs never will produce a realistic picture of the situation in those sections where these hybridizations occur. At the same time, it is obvious that there are some apomictic clones that do not hybridize, so that they may form stable distinguishable units (MENKEN & AL., 1995; Small Capitals personal communication).

More detailed studies into the nature of apomictic taxa, and into the quantitative aspects of gene flow between the ploidy levels are indispensable to complete our insight in the differentiation and speciation patterns in *Taraxacum*. This does not only hold for the common section *Ruderalia*, but holds also on a broader scale, covering other such sections as *Erythrosperma*, and including also the assumed primitive ones. A complicating factor may be that due to climatic and anthropogenic environmental changes, the distribution limits of diploid sexuals may change, rising temperatures favouring a northward expansion.

### **Section *Erythrosperma***

Within the genus, the cyclic evolutionary mechanism and thus the hybridogenous speciation may operate on a wider scale, as both ploidy levels also co-occur in other sections such as *Erythrosperma* (DEN NIJS & VAN DER HULST, 1988). Representatives of the section *Erythrosperma* basically prefer dryer and warmer habitats than *Ruderalia*, therefore their centre of distribution is more to the South, with large extensions into central and western Europe in the relatively warm and dry habitats like sand dunes and calcareous grassland sites.

Cytological data of this section make clear that triploids (and tetraploids) are very common all over the range of the section. However, there are also diploids on rather a



large scale, but compared with the *Ruderalia*, they show a distribution more restricted to the Southwest and Southeast in Europe (see Map 1, and for further details DEN NIJS & VAN DER HULST, 1988). Data from Italy are lacking so far, but it seems likely that diploids can be found there too.

As in *Ruderalia*, at least part of the populations are mixtures of diploids and polyploids, so we easily can hypothesize that the same hybridogenous processes we found in *Ruderalia*, occur also in this section. Apart from within-section hybridizations, one may also expect genetic contacts between sections, because hybrids between *Ruderalia* and *Erythrosperma* and *Palustria* (H.Lindb.) Dahlst. are recorded in literature (RICHARDS, 1970c; FÜRNKRANZ, 1961).

Table 3 presents a survey of diploid records concerning formal microspecies. Some of the type specimens are diploids. Nevertheless, the authors all have described the species, assuming that they were fully apomictic. I expect that a more thorough study of these and other species may bring to light complicated morphological and taxonomical situations, that reflect the evolutionary intricate status of the section in its sexual area.

Region	Taxon		Distribution area
Hungary: Balaton	<i>T. austriacum</i>	Soest	SE Europe
Slovakia: Bratislava	idem		
Slovakia: Bratislava	<i>T. isophyllum</i>	Hagl.	SE Europe
Spain: Aranjuez	<i>T. hispanicum</i>	H. Lindb.	Spain
Spain: Aranjuez	<i>T. marginellum</i>	H. Lindb.	Spain, Portugal, Turkey (?)
Spain: Aranjuez	<i>T. miniatum</i>	H. Lindb.	Spain, Portugal, France
Switzerland: Zürich	<i>T. rufulum</i>	Soest	Czechia, Slovakia, Bulgaria
Lebanon: Ainata	<i>T. laxum</i>	Hagl.	Lebanon
Turkey: Aranaoutkeny	<i>T. turcicum</i>	Soest	Turkey (and?)

Table 3. Diploid sexual species of *Taraxacum* section *Erythrosperma* recorded from Southern Europe. Based on DEN NIJS & VAN DER HULST (1988). In Slovakia, hybrid swarms were found in *austriacum/isophyllum* complexes, and intersectional with *Ruderalia* as well.

### Other *Taraxacum* sections present in the Mediterranean

Concluding this contribution, Table 4 gives a survey of all *Taraxacum* sections present in the Mediterranean. A total of 21 sections occur (STERK & al., 1987) and 10, possibly 11, of them contain both diploids and polyploids (STERK & al., 1987, KIRSCHNER & STEPANEK, 1993, 1994). The latter group of sections may be expected to combine both reproductive strategies. It is still largely unknown whether in these sections, as in *Ruderalia* and *Erythrosperma*, sexual and asexual individuals co-occur in populations, and whether they consequently will be able to exchange genetic material and produce viable and fit hybrids. A closer study of the population structure of

representatives of sections like these will throw light on their evolutionary dynamics, in other words, on the occurrence of hybrid phenomena, and also on the taxonomic problems related with such dynamic situations. DNA marker techniques will provide excellent tools in performing these studies.

Section	Total no. species	Ploidy levels	Reproduction	
			sexual	apomictic
<i>Glacialia</i> Hand.-Mazz.	1	2x	•	
<i>Piesis</i>	3	2x	•	(s-c)
<i>Oligantha</i> Soest	c.4	2x	•	
<i>Dioszegia</i> (Heuff.) Heuff.	3	2x	•	(s-c)
<i>Alpestris</i> Soest	c.30	2x, 3x, 4x	•	•
<i>Alpina</i> G.E. Hagl.	c.25	2x, 3x, 4x	•	•
<i>Arctica</i> Dahlst.	c.15	2x?, 3x, 4x, 5x	•	•
<i>Erythrocarpa</i> Hand.-Mazz.	c.50	2x, 3x, 4x	•	•
<i>Erythroperma</i>	c.120	2x, 3x, 4x	•	•
<i>Fontana</i> Soest	c.15	2x, 3x, 4x	•	•
<i>Orientalia</i> Hand.-Mazz.	c.30	2x, 3x	•	•
<i>Rhodotricha</i> Hand.-Mazz.	c.7	2x, 3x	•	•
<i>Ruderalia</i>	>1000 (?)	2x, 3x	•	•
<i>Scariosa</i> Hand.-Mazz.	c.15	2x, 3x, 4x	•	•
<i>Palustria</i>	c.60	3x, 4x	(•?)	•
<i>Cucullata</i> Soest	c.10	3x		•
<i>Dissecta</i> Soest	3	3x		•
<i>Obovata</i> Soest	c.3	4x, 6x		•
<i>Pachera</i> Soest	3	4x		•
<i>Rhodocarpa</i> Soest	1	3x, 4x		•
<i>Spuria</i> DC.	6	4x, 5x, 6x, 7x		•

Table 4. *Taraxacum* sections (21), occurring in the Mediterranean region and the reproductive modes present. Numbers of species are totals described per section. s-c = self-compatibility present in section; all other sexuals are self-incompatible.

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