

## Phytogeography and speciation of *Taraxacum* (Asteraceae) in East Asia

Tatuyoshi Morita

(Biological laboratory, Faculty of Education, Niigata University, 8050 Ikarashi ni-no-cho,  
Niigata-shi 950-21, Japan)

The genus *Taraxacum* includes approximately 2000 species, distributing in temperate to arctic regions mainly in the northern hemisphere (Richards, 1973). In East Asia, ca. 50 species belonging to two sections (sect. *Mongolica* and sect. *Ceratophora*) can be found; 9 from Sachalin, 8 from Kuriles, 22 from Japan, 6 from Korea, 1 from Taiwan (Kitamura, 1957), although the situation in mainland China and Russia remains obscure. According to Richards (1973), there are five areas in the world where dandelion species are highly concentrated, and Japan is one of such interesting areas for dandelion investigators.

It is well-known that *Taraxacum* forms polyploid complexes with both diploids and polyploids from triploid to decaploid ( $x=8$ ). Diploids, approximately 10% of the dandelion species (Richards, 1970a), invariably perform normal sexual reproduction. On the other hand, the majority of *Taraxacum* species are polyploid, mainly  $3x$ , and reproduce seeds asexually. Even after cutting a flower-head, it can produce complete seeds without pollination. Such a non-sexual seed formation is called agamospermy. Most polyploid *Taraxacum* obligately perform agamospermy and rare members do both agamospermy and sexual reproduction facultatively (Richards, 1970).

Embryo sac mother cells of diploid sexuals are divided into four cells through meiosis to form one megaspore. However, in polyploid agamosperms, meiosis stops at prophase and the nucleus then returns to interphase (restitution nucleus). After that, it is mitotically divided to two cells to form one megaspore. Consequently, a megaspore has  $2n$  nuclear phase (Battaglia, 1948). After embryo-sac formation, an egg cell begins embryo development without fertilization. Thus, in flower buds of agamospermous dandelions, young embryo with over hundred cells may have already grown one day before flowering (Cooper & Brink, 1949-50).

In the present paper, the following topics in the genus *Taraxacum* will be reviewed: 1) geographical distributions of the diploids; 2) clonal diversity in agamospermous polyploids; 3) paternal role of polyploids; and 4) origin of higher polyploids.

## Geographical distribution of diploid *Taraxacum* in East Asia

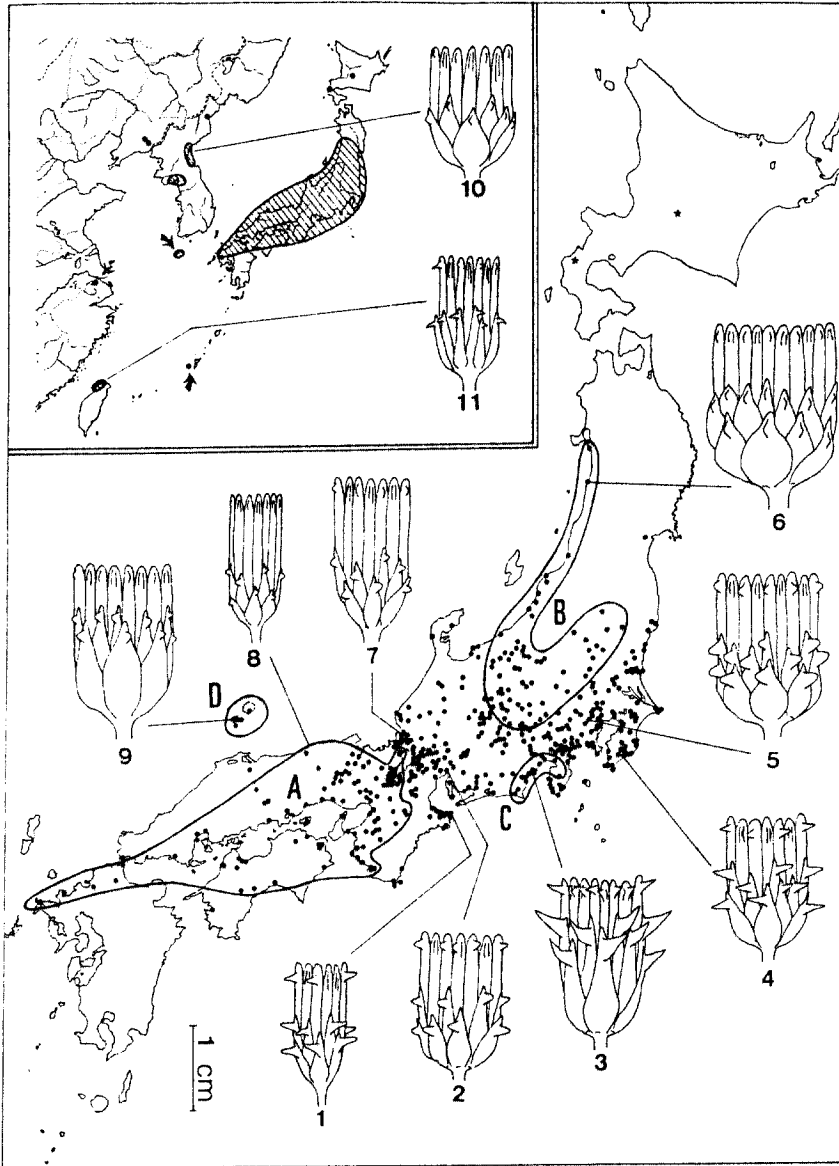
As the first step of the investigation into the processes of polyploid speciation, it is necessary to clarify the geographical structure of the polyploid complex, especially to determine the distributions of diploid entities. For clarifying their distribution, pollen assessment of herbarium specimens was carried out. Pollen size of polyploid *Taraxacum* varies from small to large, and some grains are without their contents and their exine structure is irregular. On the contrary, the pollen of diploids is regular in size and exine structure and mostly shows good content. These distinct differences were available for distinguishing the diploids and the polyploids (Morita, 1976; den Nijs & Sterk, 1980).

As a result of such pollen assessment, the percentage of diploid specimens was 51% in Japan (Morita, 1976) and 12% in other areas (Morita, 1980) of East Asia. The latter figure is similar to the mean world-wide distribution (14%) of diploid species in *Taraxacum* estimated by Richards (1970a). The conspicuously high percentage in Japan suggests that diploid *Taraxacum* in this area is particularly concentrated in the Islands of Japan.

In Japan, two kinds of diploid habitats were found (Fig. 1). One exists in the restricted localities of alpine zone in Hokkaido (*Taraxacum yuparense* Koidz. and *T. ohirense* Watanabe et Morita), and the other is a man-made habitat in the lowland of Honshu, Shikoku and Northern Kyushu. The localities of the lowland diploids are concentrated in central Honshu, where all native dandelions are diploid, whereas they are absent or sparse in northern and southern Japan (Morita, 1976). Polyploid specimens except for *T. albidum* Dahlst. were found in the lowland in northern Japan lacking the diploids and also in the mountain regions from central to western Japan (Morita, 1976). In the latter overlapping areas, habitat segregation is seen between the diploids and the polyploids. Only *Taraxacum albidum* occurs sympatrically with the diploids in the lowland of western Japan (Morita, 1976).

In the Korean Peninsula, diploid dandelions appear to have rather limited ranges of distribution as compared with those of the polyploids (Fig. 1). A few of their localities were found near Seoul (*T. hallaisanense* Nakai), near Hamhung (maybe undescribed species, although the specimens were identified as *T. ohwianum* Kitam. or *T. platyepidum* Diels), and Quelpart Isl. (*T. hallaisanense*) (Morita, 1980). In mainland China, only a few diploid localities were found, while the specimens from Taiwan were diploid (*T. formosanum* Kitam.) (Morita, 1980). It is noteworthy that every locality is either in islands or seaside areas (Fig. 1). As Malecka (1967) suggested, the present range of diploid *Taraxacum* may be glacial refuges free of ice sheet during the Würm Ice Age.

Diploid dandelions in East Asia show complex geographical variations in the flower-head morphology, especially in Japan (Fig. 1). This situation may have resulted from geographical isolation and differentiation during the ice age. Complicated variations of Japanese diploids with broad transitional zone may suggest secondary fusion through hybridization occurring as their ranges expanded. In my recent system of Japanese



**Fig. 1.** Geographical distributions and variations of involucre of diploid *Taraxacum* in East Asia. Closed circles and hatched areas indicate diploid localities of sect. *Mongolica*. Stars show diploid localities of alpine sect. *Ceratophora*. A and 8: *T. japonicum*. B and 6: *T. platycarpum* ssp. *hondoense*. 1, 2, 4, 5, 7: *T. platycarpum* ssp. *platycarpum*. C and 3: *T. platycarpum* ssp. *platycarpum* var. *longeappendiculatum*. D and 9: *T. platycarpum* ssp. *maruyamanum*. 11: *T. formosanum*. Distribution map is based on Morita (1976, 1980).

*Taraxacum* (Morita, 1995), the lowland diploids are grouped into two species, *T. japonicum* Koidz. and *T. platycarpum* Dahlst. The latter species of complex nature is treated as three subspecies and one variety (Fig. 1).

### Clonal diversity in agamospermous polyploids --- uniclonal vs. multiclonal

Polyploid dandelions are asexual reproducers. Therefore, agamospermous progeny is expected to be genetically identical to mother plants and should be uniclonal. Actually, *Taraxacum albidum* showed uniclonal composition (Menken & Morita, 1990).

This species is pentaploid ( $2n=40$ ) with distinctive white corolla. It is widely distributed in western Japan. We collected approximately a hundred plants from 12 localities and checked their clonal composition by means of enzyme electrophoresis. As a result of analysing 19 loci of 10 enzymes, they showed an identical genotype at every locus. Dr. Bachman of the University of Amsterdam checked this species by means of DNA fingerprints and also concluded that they are mostly of a single individual (personal communication). Uniclonality was also reported in *T. obliquum* (Van Oostrum *et al.*, 1985), *T. unguilobum*, *T. brachyglossum* (Hughes & Richards, 1988), *T. uliginosum* and *T. hollandicum* (Battjes *et al.*, 1992).

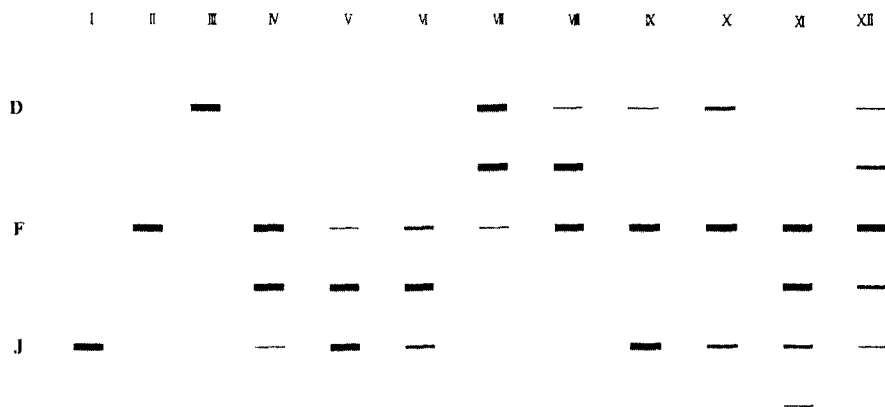
On the contrary, many polyploid dandelions (Lyman and Ellustrand, 1984; Ford & Richards, 1985; Mogie, 1985; Van Oostrum *et al.*, 1985; Hughes & Richards, 1988; Battjes *et al.*, 1992) were revealed to be multiclonal like the next example, *Taraxacum venustum* (Akhter *et al.*, 1993).

*T. venustum* Koidz. (previous *T. hondoense* Nakai ex Koidz.) is the most common dandelion species in northern Japan, growing along the roadside or surrounding paddy fields. Natural populations of *T. venustum* composed mainly of triploid, and tetraploid plants frequently grow together as well as a few pentaploid (Akhter *et al.*, 1993). For isozyme analysis, we mainly used 6-phospho-gluconate dehydrogenase (6PGD) and supplementarily two other enzymes. As 6PGD is a dimeric enzyme, we can easily determine their genotype with their dosage pattern, if we have ploidy information on the materials.

After surveying 517 *venustum* plants collected from 74 populations, 12 banding patterns at *6Pgd-1* (Fig. 2) and 21 clones by means of 3 enzyme systems were detected. It is important to recall that most *6Pgd-1* phenotypes are heterozygous (Table 1). Natural populations of *T. venustum* were sometimes uniclonal, but multiclonal populations including 2 to 4 clones were generally found (Akhter *et al.*, 1993).

European dandelions, section *Ruderalia* (commonly known as *Taraxacum officinale*) are another good example of multiclonality. Den Nijs and Sterk (1980, 1984) clarified widespread occurrence of diploid dandelions belonging to this section in central Europe. Diploid and triploid sometimes occur in the different stands, but more frequently in the

Banding pattern	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Number of plants	64	10	1	247	43	30	1	2	23	7	20	69
Frequency (%)	12.4	1.9	0.2	47.8	8.3	5.8	0.2	0.4	4.5	1.4	3.9	13.4
Number of plants with ploidy information	3X 4X 5X	20	3	1	71 8	14 4	18	1	2	11 2	7	11 38 3



**Table 1** (upper) and **Fig. 2** (lower). Schematic illustration and frequency of electrophoretic banding patterns at *6-Pgd-1* in polyploid *T. venustum* Koidz. (previous *T. hondoense*). D, F and J indicate band positions of homodimers produced by three alleles. (From Akhter *et al.*, 1993).

same stand. According to Menken *et al.* (1995), who analyzed these mixed populations enzyme-electrophoretically at three loci, triploid plants of each population include an enormous number of clones (6 to 17). Diploid plants and triploid plants from the same mixed population demonstrated very similar allelic frequencies to each other, sometimes with no significant differences by G-test. Furthermore, genotypic frequencies among the triploids surprisingly often conformed to the Hardy-Weinberg Equilibrium as well as 2X.

### Paternal role of agamospermous polyploids --- main cause of multiclonality

Why do many clones occur in clonal reproducers? The proximate cause of multiclonarity might be: 1) multiple origin of polyploids from diploid ancestors; 2) increase of clonal diversity through mutation or somatic recombination (Richards, 1986; Ellustrand & Roose, 1987); and 3) crossing events with diploid after the establishment of polyploids (Richards, 1986; Bayer, 1991; Yahara, 1990). Recent dandelion investigations have taken notice of the last scenario (Richards, 1986; Morita, Sterk & den Nijs, 1990; Battjes *et al.*, 1992; Menken

*et al.*, 1995).

As reviewed in Morita, Sterk & den Nijs (1990), many investigators have tried to make 2x-3x crosses (the former female and the latter male) in *Taraxacum* and clarified the male function of triploids (Furnkranz, 1961; Richards, 1970a, b; Muller, 1972; Jenniskens *et al.*, 1985; Hughes & Richards, 1988). Progeny plants of 2x-3x crosses were mostly diploid with a few triploids and a few tetraploids. On the basis of these crossing experiments, Richards (1986) proposed 2x-3x cycle hypothesis. Namely, diploid or triploid plants can occur cyclically in the European mixed populations through the following breeding behaviors: 1) facultative agamospermous 3x produce 2x after crossed by pollen from 2x; 2) 2x mother plants crossed by pollen from 3x produce 2x again, 3) and produce 3x. The first two processes are sometimes called rediploidization or resexualization.

My questions were whether the second process is indeed, and whether paternal genes are actually transmitted to the F1 from 2x-3x crosses. Then, we carried out crossing experiments using Asian 2x (*T. japonicum* and *T. platycarpum*, sect. *Mongolica*) as mothers and European 3x (sect. *Ruderalia*) from a French mixed population as pollen donors. Crossing experiments were done in an insect-free greenhouse of the University of Amsterdam. As diploid dandelions strongly show self-incompatibility, flower-heads of two parent plants were rubbed on each other. After the 2x-3x crosses, 80-90% of flower-heads produced seeds, although the seed setting rate per flower-head was rather low at 5-20%.

Progeny plants were grown in the greenhouse. Many gardeners and well controlled greenhouse resulted in almost a hundred percent survivorship to flower. Some 80-90% of offspring from 2x-3x crosses were 2x, confirming the previous reports.

As a genetic marker for progeny analysis, glutamate-oxaloacetate transaminase (GOT) was informative, because its electrophoretic mobility was completely different Asian and European dandelions.

Therefore, every progeny plant of crosses between them could be analyzed. Such analysis of progeny clarified that diploid progeny plants did not show any father's allele, so we decided that they were derived from selfing. Among 191 progeny plants analyzed, indeed hybrids transmitting the father's allele were only 23 in number. These plants were always polyploid, mostly eutriploid with 24 chromosomes and a few triploid aneuploid, as well as a considerable number of tetraploid (Morita, Menken & Sterk, 1990). Polyploid hybrids were obligate agamosperms except for two facultative ones.

Why did 2x mothers produce 3x and 4x progeny? The reason is found in the process of pollen formation of agamospermous polyploids. According to Battaglia (1948), the mode of pollen formation of agamospermous polyploids is slightly different from that of the megaspore formation mentioned above. Contrary to the diploid sexuals forming tetrads, chromosomes are scattered along the spindle and subsequently first division stops at diakinesis in agamospermous polyploids. This leads to random chromosome aggregation. Then each aggregate returns to an interphase nucleus (restitution nucleus), and various number of such nuclei can occur. As each nucleus is divided into two microspores,

polyploid plants produce various numbers and sizes of pollen grains. In the case of one restitution nucleus, grains must have a non-reductional chromosome number. In other cases, they may probably have a series of variously reduced chromosome numbers and of various chromosome combinations, randomly chosen from the parent's whole chromosome set.

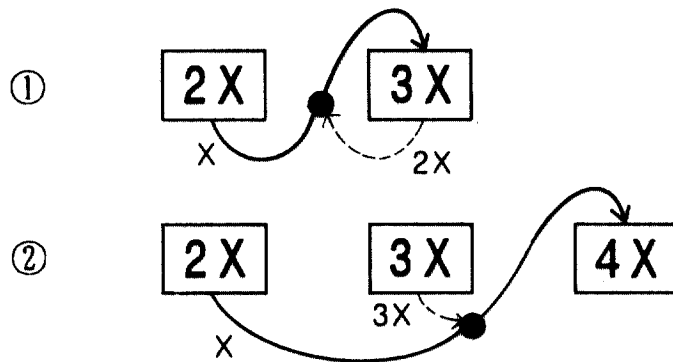
Important questions are which pollen grains of triploid actually produce viable offspring and what their chromosome number is. Chromosome numbers of indeed hybrid of  $2x-3x$  crosses strongly suggest that fertile pollen grains of  $3x$  possess 16 or nearly 16 chromosomes, as well as 24 chromosomes.

Why did diploid plants perform selfing, in spite of their strong self-incompatibility? I assume that it is due to the "recognition pollen effect" proposed by Knox (1973). Recognition pollen effect is a phenomenon that self-incompatibility will be broken, when killed or weakened compatible pollen are mixed with incompatible pollen of their own. Most pollen grains of the triploids are irregular and dead without pollen contents. And thus, they would have the recognition effect when crossed with self-incompatible diploid.

One might think that results of our crossing experiments could not be generalized, because the experiments used *Mongolica* plants as mothers instead of diploid members of the European mixed populations. However,  $3x$  male parents in our experiments were just from the mixed population of sect. *Ruderalia*. Thus, the present results provided enough information to discuss the nature of pollen from  $3x$  *Ruderalia* plants, which was the most important basis of  $2x-3x$  cycle hypothesis. If  $3x$  *Ruderalia* plants had offered fertile pollen grains with haploid chromosome set,  $2x$  indeed hybrids should have occurred from  $2x-3x$  crosses. Lack of  $2x$  indeed hybrids is a strong evidence of absence or rarity of viable pollen grains with complete (or near complete) haploid genome in  $3x$  *Ruderalia* plants. This necessarily leads to the next conclusion that no (or extremely rare) indeed  $2x$  hybrids will occur from  $2x-3x$  close relative crosses within the European mixed populations.

Now, the  $2x-3x$  cycle hypothesis needs correction. The second process, "rediploidization" through  $2x-3x$  crosses, occurs rarely if ever, although the rare possibility of "rediploidization" by facultative agamospermous triploids remains. On the other hand, the occurrence of new triploids from  $2x-3x$  crosses was confirmed. This fact indicates that  $3x$  dandelions are compilospecies, or gene burgler as called by Harlan & de Wet (1963). While the triploids have clonal reproduction as mothers, they perform sexual reproduction as pollen parents with  $2x$ , to produce new  $3x$  obtaining genes of the diploids (Fig. 3-1). The amazingly high clonal diversity of  $3x$  in European mixed populations can be understood by this mechanism.

In the case of Japanese *T. venustum*, it does not grow together with the diploids at present. But during geological time, its range must have changed and geographical isolation to the diploids may sometimes have been broken. The main cause of clonal diversity in  $3x$  *venustum* appears to be also the same in European  $3x$ . As shown in Table 1, most  $3x$  phenotypes and all  $4x$  phenotypes were heterozygous. These facts may be indirect evidence of hybrid origin of diverse  $3x$  and  $4x$  clones of *T. venustum*, probably through  $2x-3x$  crosses.



**Fig. 3.** Two main processes resulted from 2x-3x crosses in *Taraxacum*. Solid and broken lines indicate egg cell (to embryo) and sperm, respectively. Closed circles exhibit fertilization.

### Origin of higher polyploids --- a case study of *T. albidum*

As shown in the results of our crossing experiments (Fig. 3-2), new polyploids with a higher ploidy level can have originated through sexual reproduction by diploid female and polyploid male. In this chapter, the origin of *Taraxacum albidum* will be discussed as a case study of this scenario.

*T. albidum* was supposed to be of hybrid origin, because 90% of its polymorphic loci were heterozygous in isozyme electrophoresis (Menken & Morita, 1989). The hypothetical scenario is as follows: a reductional egg cell from 2x was fertilized by non-reductional sperm from 4x to give rise to 5x *T. albidum*. The problem is what the ancestral 2x and 4x species were. Isozyme analysis answered this question.

Two Japanese diploid species, *Taraxacum japonicum* and *T. platycarpum*, share almost all isozyme alleles, but only phospho-glucose isomerase (PGI) is species specific. At *Pgi-2* locus, allele A is common in both species, but B and C alleles are specific to *T. japonicum*. *T. albidum* shows 5 banded patterns with A, B and C alleles (Table 2). B and C alleles of *Pgi-2* strongly suggest that *T. japonicum* can be a candidate for the 2x female ancestor of *T. albidum*. Comparing other isozyme alleles between *T. albidum* and *T. japonicum* (Table 2), some alleles of *T. albidum* (*Lap-1* A, *Mdh* C and *Skdh* D) cannot be found in *T. japonicum*. Thus, it is considered that these alleles can be derived from the 4x male ancestor.

As such candidates of 4x ancestor, we have two species, *T. pectinatum* Kitaz. with yellow corolla and *T. hideoi* Koidz. with white or pale yellow corolla. Both species grow in the mountainous areas in West Japan. When *T. albidum* and two 4x species are compared (Table 2), three key alleles indicated by triangles are found in *T. hideoi*, but *T. pectinatum* does not possess any such alleles.



**Table 2.** Comparison of alleles at four loci among *T. albidum* and other *Taraxacum* species. Presence of alleles is shown by circles and absence by bars.

Locus	Allele	<i>T. albidum</i>	2x species		4x species	
			<i>T. japonicum</i>	<i>T. platycarpum</i>	<i>T. pectinatum</i>	<i>T. hideoi</i>
<i>Pgi-1</i>	A	○	○	○	○	○
	B	○	○	—	—	○
	C	○	○	—	—	—
	D	—	—	○	—	—
<i>Lap-1</i>	A	○◀	—	—	—	○◀
	B	○	○	○	○	○
<i>Mdh</i>	C	○◀	—	—	—	○◀
	E	○	○	○	○	○
	Other	—	○	○	—	—
<i>Skdh</i>	C	○	○	○	○	○
	D	○◀	—	—	—	○◀
	Other	—	—	○	—	—

**Table 3.** Hypothetical origin of each allele of *T. albidum*. Circles and bars are same as in Table 2.

Locus	Allele	<i>T. japonicum</i>	<i>T. albidum</i>	<i>T. hideoi</i>
		2x	5x	4x
<i>Pgi-1</i>	A	○	○ ←	○
	B	○	○ ←	○
	C	○ →	○	—
	D	—	—	—
<i>Lap-1</i>	A	—	○ ←	○
	B	○ →	○ ←	○
<i>Mdh</i>	C	—	○ ←	○
	E	○ →	○ ←	○
	Other	○	—	—
<i>Skdh</i>	C	○ →	○ ←	○
	D	—	○ ←	○
	Other	—	—	—

Table 3 shows the tentative conclusion. Alleles possibly derived from *T. japonicum* and those from *T. hideoi* are indicated by arrows in this table. *T. albidum* may have originated probably by one time hybridization between *T. japonicum* as the mother and *T. hideoi* as the father.

### Acknowledgements

I wish to thank the plant taxonomic society of Korea and the President, Dr. Sangtae Lee, for making it possible to publish this paper. I am also grateful to my coloborators, Dr. Adri A. Sterk, Dr. Steph B. J. Menken, Dr. Hans (J.) C. M. den Nijs and Dr. Shamima Akhter.

### Literature Cited

- Akhter, S., Morita, T. & Yoshida, Y. 1993. Clonal diversity in the agamospermous polyploids of *Taraxacum hondoense* in northern Honshu, Japan. *J. Plant Res.* 106: 167-179.
- Battaglia, E. 1948. Ricerche sulla parameiosi restituzionale nel genere *Taraxacum*. *Caryologia* 1: 1-47.
- Battjes, J., Menken, S. B. J. & Nijs H. C. M. den. 1992. Clonal diversity in some microspecies of *Taraxacum* sect. *Palustria* (Lindb. fil.) Dahlst. from Czechoslovakia. *Bot. Jahrb. Syst.* 114: 315-328.
- Bayer, R. J. 1991. Patterns of clonal diversity in geographically marginal populations of *Antennaria rosae* (Asteraceae: Inuleae) from subarctic Alaska and Yukon territory. *Bot. Gaz.* 152: 486-493.
- Cooper, D. C. & Brink R. A. 1945-50. The endosperm-embryo relationship in an autonomous apomict, *Taraxacum officinale*. *Bot. Gaz.* 111: 139-153.
- Ellustrand, N. C. & Roose, M. L. 1987. Patterns of genotypic diversity in clonal plant species. *Am. J. Bot.* 74: 123-131.
- Ford, H. & Richards, A. J. 1985. Isozyme variation within and between *Taraxacum* agamospecies in a single locality. *Heredity* 55: 289-291.
- Füruncranz, D. 1961. Cytogenetische Untersuchungen an *Taraxacum* im Raume von Wien 2. Hybriden zwischen *T. officinale* und *T. palustre*. *Oster. Bot. Z.* 108: 408-425.
- Harlan, J. R. & de Wet, J. M. J. 1963. The compilospecies concept. *Evolution* 17: 491-501.
- Hughes, J. & Richards, A. J. 1988. The genetic structure of populations of sexual and asexual *Taraxacum* (dandelions). *Heredity* 60: 161-171.
- Jenniskens, M. J., Nijs, J. C. M. den & Sterk, A. A. 1985. Crossability and hybridization of taxa of *Taraxacum* section *Taraxacum* from central and western Europe. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, series C* 80: 297-338.
- Kitamura, S. 1957. *Compositae Japonicae, pars sexta*. *Mem. Coll. Sci. Univ. Kyoto Ser. B.*, 24: 1-42.
- Knox, R. B. 1973. Pollen wall proteins: pollen-stigma interactions in ragweed and *Cosmos* (Compositae). *Journ. Cell Science* 12: 421-443.
- Lyman, J. C. & Ellustrand, N. C. 1984. Clonal diversity in *Taraxacum officinale*

- (Compositae), an apomict. *Heredity* 53: 1-10.
- Malecka, J. 1967. Cytoembryological studies in *Taraxacum scanicum* Dt. *Acta Biol. Crac. ser. Bot.* 10: 195-206.
- Menken, S. B. J. & Morita, T. 1989. Uniclonal population structure in the pentaploid obligate agamosperm *Taraxacum albidum* Dahlst. *Plant Species Biol.* 4: 29-36.
- Menken, S. B. J., Smit E. & Nijs H. C. M. den. 1995. Genetical population structure in plants: gene flow between diploid sexual and triploid asexual dandelions (*Taraxacum* section *Ruderalia*). *Evolution* (in press).
- Mogie, M. 1985. Morphological, developmental and electrophoretical variation within and between obligately apomictic *Taraxacum* species. *Biol. J. Linn. Soc.* 24: 207-216.
- Morita, T. 1976. Geographical distribution of diploid and polyploid *Taraxacum* in Japan (in Japanese with English summary). *Bull. Natn. Sci. Mus., Ser.B (Bot.)*, 2: 23-38.
- Morita, T. 1980. A search for diploid *Taraxacum* in Korea and eastern China, by means of pollen observations on herbarium specimens. *Journ. Jap. Bot.* 55: 1-12.
- Morita, T. 1995. *Taraxacum*. New flora of Japan. Kodansha, Tokyo (in press).
- Morita, T., Menken, S. B. J. & Sterk, A. A. 1990. Hybridization between European and Asian dandelions (*Taraxacum* section *Ruderalia* and section *Mongolica*) 1. Crossability and breakdown of self-incompatibility. *New Phytol.* 114: 519-529.
- Morita, T., Sterk, A. A. & Nijs J. C. M. den. 1990. The significance of agamospermous triploid pollen donors in the sexual relationships between diploids and triploids in *Taraxacum* (Compositae). *Plant Species Biol.* 5: 167-176.
- Müller, U. 1972. Zytologisch-embryologische Beobachtungen an *Taraxacum*- Arten aus der sektion *Vulgaria* Dahlst. in der Schweiz. Bericht über das Geobotanische Forschungsinstitut ETH, Stiftung Rubel in Zurich 41: 48-55.
- Nijs, J. C. M. den & Sterk, A. A. 1980. Cytogeographical studies of *Taraxacum* (=sect. *Vulgaria*) in central Europe. *Bot. Jahrb. Syst.* 101: 527-554.
- Nijs, J. C. M. den & Sterk, A. A. 1984. Cytogeography of *Taraxacum* sectio *Taraxacum* and sectio *Alpestris* in France and adjacent parts of Italy and Switzerland, including some taxonomic remarks. *Acta Bot. Neerl.* 33: 1-24.
- Richards, A. J. 1970a. Eutriploid facultative agamospermy in *Taraxacum*. *New Phytol.* 69: 761-774.
- Richards, A. J. 1970b. Hybridization in *Taraxacum*. *New Phytol.* 69: 1103-1121.
- Richards, A. J. 1973. The origin of *Taraxacum* agamospecies. *Bot. J. Linn. Soc.* 66: 189-211.
- Richards, A. J. 1986. *Plant Breeding Systems*. George Allen and Unwin, London.
- Van Oostrum, H., Sterk, A. A. & Wijsman, H. J. W. 1985. Genetic variation in agamospermous microspecies of *Taraxacum* section *Erythrosperma* and section *Obliqua*. *Heredity* 55: 223-228.
- Yahara, T. 1990. Evolution of agamospermous races in *Boehmeria* and *Eupatrium*. *Plant Species Biol.* 5: 183-196.