

## SEXUAL AND AGAMOSPERMOUS TARAXACUM SPECIES IN THE NETHERLANDS

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### SUMMARY

A careful examination of 489 herbarium specimens of Dutch dandelions, identified by specialists and referred to 161 species of *Taraxacum*, strongly suggested that four of these taxa might be sexual diploids. The occurrence of diploid individuals of *T. limburgense* (sect. *Vulgaria*) was confirmed by chromosome counts. Facultative agamospermy may occur in 17 other species of that section. The specimens of the sections *Erythrosperma*, *Obliqua*, *Palustris* and *Spectabilia* studied did not indicate the incidence of sexuality or facultative agamospermy in these taxa in The Netherlands; as far as can be ascertained they are all triploid and agamospermous.

The possible consequences of the occurrence of sexuality in connection with variation-patterns and processes of speciation within the genus *Taraxacum* in The Netherlands are concisely discussed.

### 1. INTRODUCTION

The increased interest in the taxonomy of the genus *Taraxacum* originated by the turn of the century in Sweden and Denmark when OSTENFELD (1899) and RAUNKIAER (1903) demonstrated its special mode of reproduction. Ostensfeld discovered dandelions without pollen which nevertheless produced seeds, and Raunkiaer showed that also castrated and bagged-in flowers yield viable seeds. Both workers concluded that the seeds are formed by agamospermy. This suggestion was soon confirmed by means of cytological studies, e.g. by MURBECK (1904). The inquiry into *Taraxacum* rapidly became intensified and taxonomists began to distinguish narrowly defined microspecies, whose numbers increased at a fast rate. At present the number of described species in Europe is estimated as about 1500 divided over 21 sections (RICHARDS & SELL 1976). *Taraxacum* forms a polyploid complex with the basic chromosome number  $x = 8$ . According to an estimate by DOLL (1977) about 10% of the species is diploid ( $2n = 16$ ), about 45% triploid ( $2n = 24$ ), about 28% tetraploid ( $2n = 32$ ) and about 5% pentaploid ( $2n = 40$ ); higher ploidy levels are extremely rare. The number of aneuploid species is strikingly large (about 11%). So far all diploid species proved to be sexual and the polyploids agamospermous. The latter reproduce principally by diplosporic diploid parthenogenesis, a form of agamospermy in which the female gametes originate from a restitutional meiosis and these diploid egg cells give rise to new individuals without a fertilisation having taken place (RUTISHAUSER 1967, STERK & DEN NIJS 1978). The agamospermy is supposed to be responsible for a complete genetic isolation of closely related species, providing the basis of the taxonomic identity of the species.

However, some authors have shown that in agamospermous triploid populations occasionally sexual reproduction, and consequently an exchange of genes, may take place. In this case we find in a population, apart from an obligatory form, also a facultative type of agamospermy.

The most common and most varied sections of *Taraxacum* found in Europe are considered to be relatively young and advanced in a phylogenetic sense, and supposed to be almost completely polyploid and agamospermous. The sections in question are principally *T. sect. Vulgaria* (with about 1200 microspecies), *sect. Palustria* (with about 50 species), *sect. Spectabilia* (with about 250 species), *sect. Erythrosperma* (with about 120 species) and some alpine sections such as *T. sect. Alpestris* (with about 30 species), *sect. Alpina* (with about 25 species), *sect. Fontana* (with about 15 species) and *sect. Cucullata* (with about 10 species).

Diploids are said to be very common in the phylogenetically "older" sections of the genus and to occur particularly in western Central Asia where the centre of origin is supposed to be located (RICHARDS 1973). Also in southern Europe a number of diploid and self-incompatible taxa belonging to more or less primitive sections and with usually limited areas of distribution have been discovered, possibly as relicts (RICHARDS 1973; DOLL 1974, 1977).

However, also in the more advanced sections *Erythrosperma* and *Vulgaria* sexual diploids were discovered in Europe. Till recently scattered localities of a few species were known, namely from southern Sweden, Austria, Switzerland, England, and the G.D.R. (DEN NIJS & STERK 1980 for a survey), but the latest studies (DEN NIJS & STERK, l.c. and in prep.) have shown that sexual plants of populations of the *sect. Vulgaria* are of common occurrence in Central and southern Europe. Such populations have a characteristic distribution. South of a zone passing through Europe from W. to E. diploid and sexual individuals of *Vulgaria* occur more or less commonly, usually in mixed populations with triploid agamospermous individuals. This zone runs roughly from Nantes in the W. via Orléans and Nancy in France to Karlsruhe and Regensburg and continues to the Czechoslovakian-G.D.R. border. To the N. of this zone diploids are almost non-existent and most populations are polyploid and agamospermous as mentioned above.

The Netherlands are situated in the "agamospermous" area and it was not to be expected that sexual diploids are present. A thorough study of the reproduction had hardly been attempted, however, and what became known was deduced mainly from chromosome counts (HOU-LIU 1963; DEN NIJS, STERK & VAN DER HAMMEN 1978). The present investigation was intended to establish whether sexuality in *Taraxacum* occurs at all in this country, and if so, to obtain some insight into the incidence of this form of reproduction.

## 2. METHODS

The inquiry into the incidence of sexuality and agamospermy is largely based on assessments of the pollen. TSCHERMAK-WOESS (1949) discovered that sexual diploid and asexual polyploid dandelions produce characteristically different kinds of pollen: diploid individuals produce, through a normal meiosis, pollen of uniform and but little variable size, whereas polyploids (and particularly) triploids, owing to a strongly disturbed meiosis, produce pollen grains with a very variable diameter. It appeared to be possible, with a high degree of reliability, to distinguish diploids from triploids on the basis of these pollen characteristics (RICHARDS 1968, MORITA 1976, 1980, DEN NIJS EN STERK 1980). A complication may occur in triploid and facultatively agamosperous individuals. In these agamosperms in a single head florets may occur with a rather normal meiosis which may result in the production of regular and but little variable pollen grains next to florets with a strongly disturbed meiosis which yields extremely variable pollen grains. In cases of agamospermy with many normal meioses it may prove to be difficult or altogether impossible to decide whether a plant is diploid and sexual or triploid and facultatively agamosperous (RICHARDS 1972). Especially in doubtful cases it is absolutely necessary to establish or to verify the ploidy level by means of chromosome counts.

The principal advantages of the pollen method are that it is a rapid one and that it can be applied to heads in the bud stage, also in herbarium material in order to establish the mode of propagation and accordingly the ploidy level.

Pollen slides were made by suspending the pollen in polyvinyl-lactophenol which has a sufficiently high viscosity (to prevent compression of the grains by the cover glass). As a staining agent trypane blue was added, so that the grains filled with cytoplasm were dyed blue and those without cytoplasm remained unstained and the percentage of undeveloped, sterile pollen grains per plant could easily be determined.

Methaphase mitotic preparations were obtained by applying the squash technique to root tips, using basic fuchsin as the staining agent; they were studied by using phase contrast microscopy (see DEN NIJS et al. 1978).

## 3. MATERIAL

Of 489 named herbarium specimens of *Taraxacum* collected in The Netherlands and kept in the Rijksherbarium, Leiden (L) and in the Van Soest Herbarium incorporated in L, the variation in pollen size was studied. All identifications were made by A. Hagendijk, Professor J. L. van Soest and H. A. Zevenbergen. The taxonomy and nomenclature is according to HAGENDIJK et al. (1975, and in the press).

In table 1 the distribution of the 489 plant specimens over the sections of *Taraxacum* is shown. This table shows that all species or at least a large number of species of the various sections were examined; those not included in the investigation are mostly the very rare ones (and often did not have inflor-

Table 1. Distribution of specimens studied over the section of *Taraxacum*.

Section	No. of species recorded from the Netherlands	No. of species studied	No. of specimens studied
Erythrosperma	23	17	55
Obliqua	1	1	4
Palustria	10	7	18
Spectabilia	9	6	16
Vulgaria	153	130	396
Total	196	161	489

escence buds in the herbarium specimens). The number of plants per species was usually not excessive.

In Zuid-Limburg (Mechelen/Geul), as a sequel to the examination of herbarium specimens, from a meadow in a stream valley 12 living plants of *T. limburgense* were collected in the spring of 1981 for chromosome studies in addition to a population sample of about 50 flowering heads for pollen studies preserved in 70% ethanol. A second sampling of 30 flowerheads took place in September 1981, in the autumn-flowering period.

#### 4. RESULTS OF THE HERBARIUM SCREENING

##### 4.1. A classification of the pollen-variation patterns

A preliminary classification for the Dutch species was made in which the following four categories are distinguished:

1. PR. Pollen very regular and varying but little in diameter (between 30  $\mu\text{m}$  and 40  $\mu\text{m}$ , with a mean of about 35  $\mu\text{m}$  and a s.d. < 3). An example of this type is the pollen of *T. limburgense* (fig. 1). This type PR is found in diploid sexual plants with a regular meiosis.
2. PI. Pollen clearly irregular and varying strongly in diameter from 15  $\mu\text{m}$  to 70  $\mu\text{m}$ , with a mean of usually between 35–40  $\mu\text{m}$  and a s.d. > 3. An example is provided by *T. ancistrolobum* (fig. 2) and *T. croceiflorum* (fig. 3). This type is characteristic of triploid agamospermous plants with a strongly disturbed meiosis.
3. PT. Pollen upon the whole of regular size but containing some deviating grains. The mean size and the s.d. approximate those of type PR. An example is provided by triploid plants of *T. croceiflorum* in fig. 4. It is not yet clear what reproductive system operates in such plants, but conceivably this type is indicative of facultatively agamospermous plants with a relatively large number of regular pollen produced by frequent, normal reductional meioses (compare RICHARDS 1970, 1973).
4. PA. Pollen totally absent. The plants are triploid and obligatorily agamospermous.

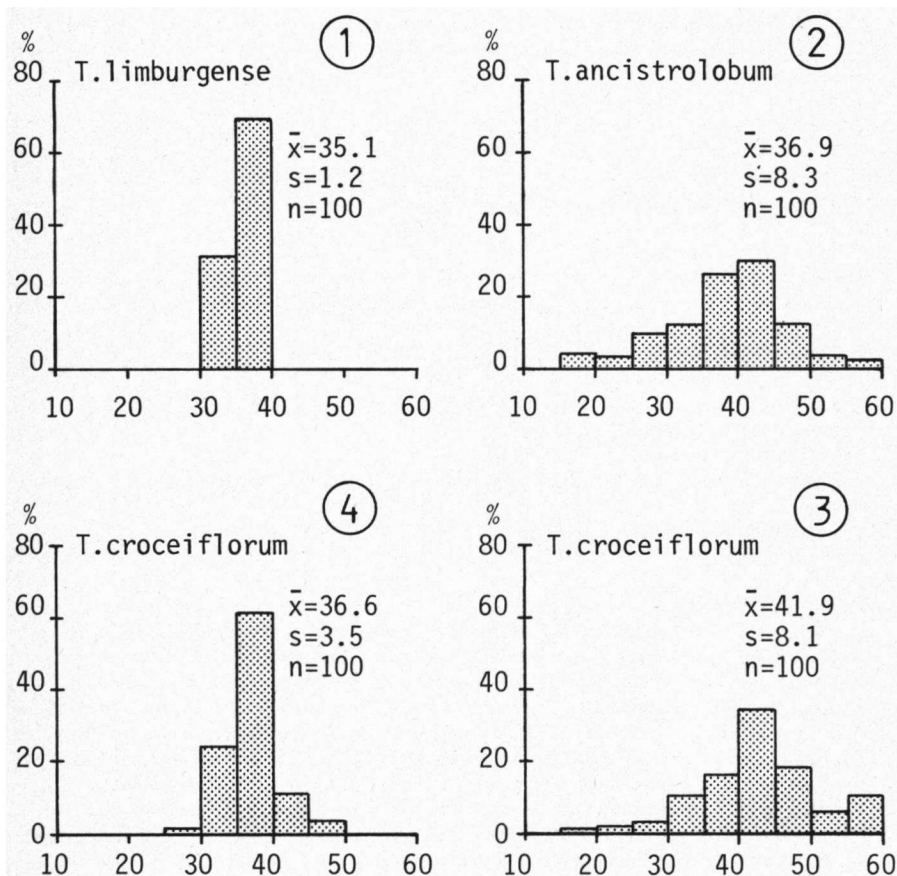


Fig. 1-4. Frequency distributions of pollen of selected species.

In 5 individuals relatively large pollen grains were found with an average diameter of 40–55  $\mu\text{m}$  and in three of the cases of very regular size. Presumably these plants were tetraploids. They were identified as *T. anglicum* (*Spectabilia*), *T. fagerstroemii* (*Vulgaria*), *T. fulgidum* (*Vulgaria*) and *T. singulare* (*Vulgaria*).

#### 4.2. Classification of the species on the basis of the pollen variation

In the following survey the distribution of the various species over the different pollen types is indicated, the number of plants examined being mentioned between brackets. Sometimes specimens referred to the same species exhibit different pollen types.

Section ERYTHROSPERMA (17 species)

1. Pollen type PI (14 species)

*T. agaurum* (3), *T. aphanochroum* (1), *T. brachyglossum* (3), *T. commixtum* (4), *T. disseminatum*

- (3), *T. dunense* (4), *T. lacistophyllum* (5), *T. laetiforme* (3), *T. oxoniense* (3), *T. rubicundum* (5), *T. scanicum* (5), *T. subdissimile* (1), *T. tanyolobum* (1), *T. tortilobum* (4).
2. Pollen type PA (2 species)  
*T. silesiacum* (5), *T. taeniatum* (2).
3. Pollen types PI and PA (1 species)  
*T. proximum* (PI: 1; PA: 2).
- Section OBLIOUA (1 species)
1. Pollen type PI (1 species)  
*T. obliquum* (4).
- Section PALUSTRIA (7 species)
1. Pollen type PI (5 species)  
*T. austrinum* (3), *T. crassiceps* (1), *T. friscum* (2), *T. gelricum* (2), *T. hollandicum* (5).
2. Pollen types PI and PA (1 species)  
*T. palustre* (PI: 1; PA: 2).
3. Pollen type PA (1 species)  
*T. maritimum* (2).
- Section SPECTABILIA (6 species)
1. Pollen type PI (5 species)  
*T. anglicum* (2), *T. euryphyllum* (2), *T. hygrophilum* (2), *T. johannis-janssenii* (3), *T. zevenbergenii* (1).
2. Pollen type PA (1 species)  
*T. nordstedtii* (5).
- Section VULGARIA (130 species)
1. Pollen type PI (106 species)  
*T. aberrans* (6), *T. acutangulum* (1), *T. acutifidum* (1), *T. adamii* (6), *T. aequilobum* (2), *T. akteum* (4), *T. amplum* (4), *T. ancistrolobum* (5), *T. arenarium* (3), *T. armatifrons* (1), *T. atactum* (5), *T. atonolobum* (4), *T. atrovirens* (4), *T. aurosulum* (1), *T. brabanticum* (1), *T. bracteatum* (5), *T. calochroum* (4), *T. canoviride* (2), *T. chlorodes* (4), *T. christiansenii* (1), *T. cophocentrum* (3), *T. copidophyllum* (2), *T. cordatum* (3), *T. corynodiiforme* (4), *T. crispifolium* (1), *T. cyanolepis* (3), *T. dilaceratum* (1), *T. effusum* (2), *T. ekmaniiiforme* (2), *T. excellens* (4), *T. exertum* (4), *T. fagerstroemii* (3), *T. fictum* (1), *T. filidens* (1), *T. fridenii* (1), *T. fulgidum* (2), *T. hamatulum* (5), *T. hamatum* (5), *T. hebelobum* (1), *T. hemipolyodon* (1), *T. horridum* (1), *T. inarmatum* (2), *T. incisiforme* (2), *T. incomptum* (1), *T. infestum* (4), *T. insigne* (2), *T. kernianum* (6), *T. lacerifolium* (6), *T. laciniatifrons* (2), *T. laeticolor* (2), *T. lamprophyllum* (5), *T. lancidens* (5), *T. lingulatum* (1), *T. lucidum* (6), *T. matricium* (1), *T. melanthoides* (3), *T. molybdolepis* (1), *T. monochroum* (2), *T. multicolorans* (2), *T. multifidum* (1), *T. nitidum* (4), *T. nubilum* (1), *T. obliquilobum* (3), *T. olitorium* (5), *T. ordinatum* (3), *T. pachymeroides* (3), *T. pallidipes* (1), *T. pannulatiforme* (3), *T. pannulatum* (2), *T. pectinatiforme* (4), *T. piceatum* (2), *T. planum* (6), *T. ploegii* (4), *T. polyodon* (5), *T. porrigens* (1), *T. prionoides* (1), *T. prionum* (2), *T. pseudacrolobum* (2), *T. quadrans* (6), *T. railonsalae* (1), *T. raunkiaeri* (5), *T. recessum* (1), *T. replicatum* (2), *T. rigens* (2), *T. rubrisquameum* (2), *T. sagittipotens* (3), *T. severum* (4), *T. sinuatum* (2), *T. stenoschistoides* (2), *T. stereodes* (2), *T. subcyanolepis* (3), *T. subericinum* (5), *T. subhamatum* (5), *T. sublacerifolium* (5), *T. sublaeticolor* (5), *T. subpraticola* (3), *T. tarachodum* (4), *T. tenebricans* (3), *T. tenue* (1), *T. tenuiceps* (1), *T. texelense* (1), *T. tortuosum* (3), *T. trilobatum* (5), *T. undulatiflorum* (3), *T. undulatum* (3), *T. vastisectiforme* (1).
2. Pollen types PI and PT (16 species)  
*T. dahlstedtii* (PI: 1; PT: 3), *T. ekmanii* (PI: 4; PT: 1), *T. eudontum* (PI: 3; PT: 1), *T. falciferum* (PI: 2; PT: 1), *T. flandricum* (PI: 1; PT: 1), *T. flevoense* (PI: 1; PT: 1), *T. haematicum* (PI: 3; PT: 1), *T. hamatiforme* (PI: 5; PT: 1), *T. longisquameum* (PI: 1; PT: 1), *T. marklundii* (PI: 5; PT: 1), *T. oblongatum* (PI: 1; PT: 1), *T. pachymerum* (PI: 4; PT: 1), *T. pannucium* (PI: 4; PT: 1), *T. planoides* (PI: 3; PT: 2), *T. sellandii* (PI: 5; PT: 1), *T. subdivitum* (PI: 5; PT: 1).
3. Pollen type PR (2 species)  
*T. angustisquameum* (1), *T. limburgense* (1).
4. Pollen types PI and PR (1 species)  
*T. alatum* (PI: 5; PR: 1).

5. Pollentypes PI, PR and PT (PI: 5; PR: 1; PT: 1).

6. Pollen type PA (3 species)

*T. excertiforme* (1), *T. ostensfeldii* (2), *T. speciosum* (3).

These data make it quite clear that the incidence of sexuality among the specimens of the sections *Erythrosperma*, *Obliqua*, *Palustria* and *Spectabilia* is most unlikely. The *Vulgaria* exhibit a different picture: among specimens of four species pollen of the PR type was found, namely in *T. alatum*; *T. angustisquameum*, *T. croceiflorum* and *T. limburgense*. This is suggestive of the presence of diploid and sexual individuals in populations of these species.

## 5. RESULTS OF THE FIELD STUDY

An investigation into the ploidy level and sexuality was carried out with material of *T. limburgense*. The herbarium specimen (herb. Van Soest 24835) previously examined had been collected at a locality south of the river Geul near Mechelen in Zuid-Limburg. In a meadow covering both sides of the Geul, just a little to the S. of Mechelen (fig. 5) this species was rediscovered and identified by A. Hagendijk and H. A. Zevenbergen.

The pollen of the 12 plants of *T. limburgense* collected at that site belonged to type PR. Chromosome counts of material from nine individuals confirmed their diploid status:  $2n = 16$  (see fig. 6).

An analysis of a *Taraxacum* population sample of 50 flowerheads collected aselectively in the whole plot yielded the following result: 58% of the individuals had the pollen type PR and were in all probability also diploid. It follows that the majority of the dandelion flora of that meadow consists of diploids.

The analysis of the autumn sample of flowerheads brought to light that only PI pollen was present, so that apparently only triploid, asexual individuals come into flower again in the autumn. Whether this is an exceptional or regular pattern in the mixed populations and the possible consequences with respect to the reproductive strategies of the different cytotypes (taxa), are still under investigation.

Considering that the spring sample was aselectively taken one may assume that other species than *T. limburgense* were present but for the time being it is not known which taxa are involved. The available data render the diploid and sexual condition of the other herbarium specimens with the PR pollen type more than likely. They include *T. alatum* from the St. Pietersberg (province of Limburg) and *T. angustisquameum* found near Epen (also Zuid-Limburg) and *T. croceiflorum* collected in two localities, viz., near Ommen (province of Overijssel) and near Elst (province of Utrecht) (fig. 5).

In a phytogeographical context it is noteworthy that of the 5 diploid or presumably diploid specimens three hailed from Zuid-Limburg (in the "Krijt District") and two from the "Fluviatiel District" (HEUKELS-VAN OOSTSTROOM 1977). Both districts have phytogeographical and ecological relations with Central Europe. It is possible that the previously recorded diploids of section *Vulgaria* from C. Europe are geographically and phylogenetically linked with

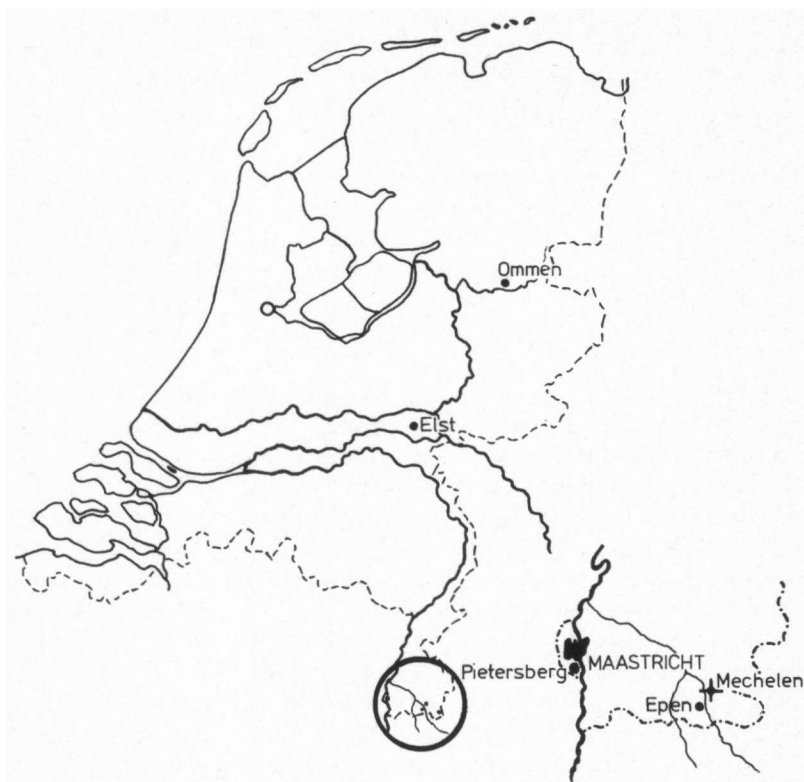


Fig. 5. Distribution of the PR-pollen specimens and the diploid Mechelen population (+).

the presently discovered diploid forms of The Netherlands. A more thorough investigation is required to ascertain whether the occurrence of diploid dandelions in The Netherlands is restricted to the two above-mentioned Districts.

The number of herbarium specimens exhibiting the pollen type PT is surprisingly high. Such plants might be facultative agamosperms (RICHARDS 1970, 1972). The 21 individuals were referred to 17 (micro)species. They were phyto-geographically distributed as follows: "Duin District" 3, "Fluviatiel District" 4, "Gelders District" 6, "Haf District" 6, "Kempens District" 2. This does not

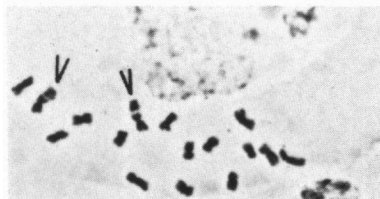


Fig. 6. Roottip metaphase plates of *T. limburgense* from Mechelen/Geul. Note the characteristic secondary constrictions (arrows).

permit any definite conclusions but at any rate these putative facultative agamosperms are not restricted to Limburg or the "Fluviatiel District".

Of *T. alatum* specimens with the PR type and individuals with the PI type were encountered, and in *T. croceiflorum* even three types of plants with the pollen types PR, PT and PI, respectively. This renders the incidence of diploid and sexual, and of triploid and agamospermous individuals within these species highly probable, which may be indicative of the occurrence of facultative agamospermy in these species (RICHARDS 1970). Such a form of agamospermy may conceivably link diploid and triploid cytotypes through hybridisation.

## 6. DISCUSSION

The present report had the following drawbacks:

- (1) not all species were studied,
- (2) the number of individuals and of localities per species is low (upon the average about 3),
- (3) the pollen size variation still cannot be interpreted unambiguously.

In spite of these restrictions our inquiry has yielded cogent evidence of the occurrence of sexuality among *Taraxacum* in The Netherlands. Our studies did not provide indications of the incidence of diploid sexual forms in the sections *Obliqua*, *Palustria*, *Spectabilia* and *Erythrosperma*. This is in good agreement with the published records from northern Europe, *T. brachyglossum* (sect *Erythrosperma*) excepted. Of this species in England diploid and sexual individuals were found, although only occasionally, next to triploid and (both obligatorily and facultatively) agamospermous ones (RICHARDS 1970, 1972). Since only a few specimens of *T. brachyglossum* were included in our investigation the future discovery of diploids of this taxon in The Netherlands is not impossible (see DEN NIJS et al. 1978).

In the section *Vulgaria*, on the other hand, at least one diploid and sexual species was found, viz., *T. limburgense*, and three other species almost certainly contain such diploids, viz. *T. alatum*, *T. angustisquameum* and *T. croceiflorum*. According to previous reports both *T. alatum* and *T. croceiflorum* would be triploid. In addition, in 21 specimens referred to 17 species PT pollen patterns were found, which points to facultative agamospermy and, hence, to partial sexuality.

The incidence of sexuality, even if only to a small extent, may have important consequences for the identity of the microspecies of *Taraxacum* and for the micro-evolution of the group, mainly as a result of hybridisation. Hybrids between sexual microspecies belonging to the same section or even to different sections have been produced experimentally and are also found in nature (RICHARDS 1973). Also diploid sexual and triploid (facultatively or obligatorily) agamospermous taxa may hybridise and such hybrids occur in nature (RICHARDS 1970). It is noteworthy in this connection that so far natural hybridisation has only been recorded when diploid and sexual plants were present. Now that sexual diploids have been discovered in The Netherlands, their oc-

currence may have an important bearing upon the variation and the taxonomic identity of the Dutch dandelions, and may conceivably even yield new variants. The rate of incidence of sexuality, its possible restriction to certain taxa, and the question whether its presence can be ecologically and/or geographically characterised are under investigation.

As mentioned in the introductory chapter The Netherlands lie within the "agamospermous" area, but the present study shows that also sexual plants occur in this region. Previously sexual individuals of *T. obtusilobum* (sect. *Vulgaria*) had been found in southern Sweden (GUSTAFSSON 1937). Also in Britain sexual individuals have been recorded; according to RICHTARDS (1972) *T. subcyanolepis* (sect. *Vulgaria*) is an indigenous sexual species in England. (However, in The Netherlands of *T. subcyanolepis* so far only triploid agamospermous individuals have been encountered.)

In England, by means of a survey of 195 populations from 31 vice-counties, in eight populations sexual diploids were found in taxa belonging to the sections *Vulgaria* and *Erythrosperma* (VALENTINE & RICHARDS 1967); a follow-up showed that also hybridisation and introgression takes place.

It would seem as if the border zone in Central Europe separating the mainly "sexual" range from the "agamospermous" one is only roughly indicative of the actual situation, which was to be expected considering the method of sampling. In view of the present data, diploids may well occur much farther to the north in a diffuse distribution pattern than was hitherto assumed, and conceivably may locally be found in appreciable numbers. The corollary of these findings is that by means of hybridisation actual processes of speciation may continue to take place within the asexual and, supposedly, genetically more or less constant microspecies complex of *Taraxacum* in north-western Europe. More detailed inquiries may eventually yield a more precise insight into the taxonomic, phytogeographical and ecological interrelationships of sexuality and agamospermy in western Europe.

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