# CYTOGEOGRAPHY OF TARAXACUM SECTIO TARAXACUM AND SECTIO ALPESTRIA IN FRANCE AND ADJACENT PARTS . OF ITALY AND SWITZERLAND, INCLUDING SOME TAXONOMIC REMARKS 

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#### Abstract

SUMMARY In France and adjacent parts of Italy and Switzerland the distribution of diploid and triploid specimens of Taraxacum (mainly) sect. Taraxacum has been established on the basis of about 200 population samples and of herbarium specimens (c. 5,500 individuals in all). Most diagnoses are based on pollen characteristics, a minority on chromosome counts. Triploids are common throughout France. Diploids occur in the major part of the area with a relative frequency per population of 3 to $100 \%$; they become more common southward from Le Mans-Tours-Strasbourg. Some data from the northern region suggest that there may be a broad transitional zone (towards total absence of diploids), reaching to Middle-Belgium and the Dutch South-Limburg area. To the south diploids are present in the Pyrenees and elsewhere in northern Spain, and in the Alps of Northern Italy. There are but weak indications pointing at some overall ecological differentiation between the diand triploid cytodemes.

The presence of numerous diploid, sexual species came to light of which 26 belong to sect. Taraxacum and 2 to sect. Alpestria. Some of the species occur at both the ploidy levels. One may expect that more microspecies may prove to be diploid. In the discussion attention is paid to (1) some of the evolutionary mechanisms thought to be active in the sections studied (facultative sexuality, re-diploidisation) and (2) the consequences of the present data in respect of the applicability of the microtaxonomy within the range of the distribution of the sexual diploids.


## 1. INTRODUCTION

The present contribution is a continuation of the cytogeographical inquiries carried out in Central and southern Germany and the Alpine region (compare DEN Nijs \& Sterk 1980; Jenniskens et al. 1983). The first reference includes a survey of the data pertaining to the incidence in Europe of diploid sexual and triploid agamospermous forms especially of the section Taraxacum. The principal cytogeographic conclusions of these investigations are (1) the more or less frequent occurrence of diploid individuals of the sect. Taraxacum in large parts of the Alpine region and in S. and C. Germany as far as the Odenwald and also in the northern and eastern parts of Austria; and (2) the greater rarity of diploids in the Alpine Tauern area and in a North-South running zone between Nürnberg and München, see Jenniskens et al. (1983).

Still farther to the north than the Odenwald diploids were recently encoun-
tered in the southernmost part of The Netherlands in the province of Limburg (Sterk et al. 1982).

According to Doll (1982) the diploids of the sect. Taraxacum are most probably not original archediploids and relatively primitive but more probably of secondary origin in an evolutionary sense; the di- and triploids are more or less equally advanced and can hardly be distinguished without chromosome counts.

As pointed out in an earlier paper (Den Nijs \& Sterk 1980) the possible consequences of the incidence of sexuality are considerable from a taxonomical and biological point of view. Summarised, the following points are essential:

- The applicability of the micro-species taxonomy in the "diploid" regions is questionable. This is due to the almost obligate outbreeding sexuality of the diploids. The microspecies concept is in fact for a great deal based on the genetical isolation of the asexual reproducing triploids (as clones).
- Due to the presence of facultative sexuality in some triploids a (two-directional) genetical connection with the diploids may occur (Jenniskens et al. 1983). One may hypothesize the incidence of rediploidization in diploid - triploid cycles (compare also De Wet 1971, 1980).
- The co-existence of the sexual and the asexual reproductive system in the populations mixed up of di- and triploids makes investigations necessary to what extend these both reproductive systems interfere (or compete) in the development and/or the maintenance of the populations.
The cytogeographic pattern as far as established so far, shows a disjunction in the geographical range of the diploids in the region of central Bavaria and the Tauern. Jenniskens et al. (1983) suggest that in Central and Southern Europe there is a bifocal distribution pattern of the diploids, viz., an eastern part-area, for the time being only recorded from N. and E. Austria and the adjoining part of Slovakia, and a western one with high concentrations of diploids in S. W. Germany and Switzerland. The principal goal of the present study was to find out how extensive this western area is, especially in France, so that the accumulated data can be viewed in a wider phytogeographical perspective. To this end we had at our disposal, apart form our population samples collected in the field, a collection of herbarium specimens named by specialists which opened up the possibility of a discrete taxonomic evaluation in the light of karyological data.


## 2. MATERIALS

### 2.1. Field operations

In the main flowering season of the successive years 1979 to 1981 a collection of some 150 population samples was gathered from the greater part of France (Series THM, TGT, TRL, TCH, TS 1-10). Only relatively scattered sampling took place in the following regions: the South-West (Bordeaux-Toulouse), the Western part of Brittany, and the extreme North and North-West. A small series of samples was obtained from Val d'Aosta in N.W. Italy (TS 11-17). The samples consisted of from 30 to 40 still incompletely opened capitula kept in $70 \%$
ethanol for laboratory analyses. The samples were mainly taken from meadowland with a varied intensity of uses and managements. A few were collected in much disturbed habitats such as roadsides and -banks (see also table 1). From a number of locations live plants were taken away for chromosome counts and for cultivation and hybridisation experiments.

For all above-mentioned series of population samples holds that they have been collected during field excursions by car. In this way it was possible to visit in a short period of time quite a part of the country. The sample meadows are as a matter of fact not randomly situated but systematic, i.e. along the travelling (often minor) roads (routes départementaux).

Fig. 7 is based, apart from the above-mentioned samples, also on a series of observations of smaller samples (about 50 in all) each consisting of at most 10 capitula per site, which are shown as small symbols in the figure: open circles indicate polyploids which are most likely triploids, dots indicate the presence of diploids (irrespective of their relative local frequency) in the sampled population. This series of smaller samples is largely based on field observations made during our longer collecting trips: at more or less set distances between the normal sample sites the size vaiation of the pollen of a small number of flower heads (up to 10) was analysed in the field. In this way, with only a little more effort, a denser meshwork of data was obtained. In addition, a few smaller samples were kindly provided by other botanists.

### 2.2. Herbarium material

We had the following collections at our disposal:
A. Of the Herbarium-Van Soest (incorporated in L.) about 200 sheets collected in nearly 70 localities scattered through France. A small number (13) of these had been identified partly by Dr. Van Soest himself and partly by Dr. Sahlin; this collection contains (1) material collected by Dr. Billy (Clermont-Ferrand) consisting of 9 populations samples (series TB in table I) and (2) material collected by Dr. De Bray, Brussels: the series TDB, about 60 origins each comprising 1 or 2 specimens.
B. From the Nationale Plantentuin, Brussels-Meise (BR), 138 sheets collected in Val de Bagne (Valais, Switzerland) and named by Drs. Lawalrée and Sahlin; this collection comprises 50 (micro-) species of 6 sections and contains a number of type specimens (see Sahlin 1982).
The analyses of these herbarium collections are given in Chapter 4.3.

## 3. METHODS

The samples were collected by traversing each population along imaginary lines at set distances and taking an individual or capitulum at set intervals along these lines. The ploidy levels were determined on the basis of the pollen diameter as was done in previous studies (see e.g. Tschermak-Woess 1949, Den Nijs et al. 1980, Jenniskens et al. 1983). As a rule with this methods diploid individuals

| Sample number | Locality in France | Dept. ${ }^{1}$ no. | Height m.a.s.l. | Habitat | No. of plants | Pollen diagnosis ploidy-level (\%) |  | $\begin{aligned} & \text { Pollen } \\ & >10 \% \end{aligned}$ | sterility <br> (2x only) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  | 2x | 3x |  |  |
| THM 1 | Neuilly | 02 | 150 | heavily manured pasture | 29 | - | 100 | - | - |
| THM 2 | Sézanne | 51 | - | runderal pasture | 32 | - | 100 | - | - |
| THM 3 | Bouilly | 10 | 150 | orchard meadow | 33 | - | 100 | - | - |
| THM 4 | Auxerre | 89 | 150 | little manured woodland pasture | 33 | - | 100 | - | - |
| THM 5 | Avallon | 89 | 300 | little manured pasture | 33 | 85 | 15 | - | - |
| THM 6 | Saulieu | 21 | 510 | short mowed lawn | 33 | 24 | 76 | - | - |
| THM 7 | Lucenay-L'Evèque | 71 | 390 | road-side | 33 | 12 | 88 | - | - |
| THM 8 | Colonge | 71 | 370 | abandoned grassland | 31 | 6 | 94 | - | - |
| THM 9 | Montcenis | 71 | 350 | pasture on heavy clay | 33 | 9 | 85 | 6 | - |
| THM 10 | Mont-St. Vincent | 71 | 250 | little manured pasture, many herbs | 33 | 88 | 6 | 6 | - |
| THM 11 | Cluny | 71 | 300 | orchard-meadow | 33 | 70 | 30 | - | - |
| THM 12 | Villié | 69 | 200 | vineyard, road-side | 33 | 6 | 94 | - | - |
| THM 13 | Belleville | 69 | - | heavily grazed, loam | 33 | 45 | 55 | - | - |
| THM 14 | St. Genis-Laval | 69 | - | runderal ground | 23 | - | 100 | - | - |
| THM 15 | Annonay | 07 | 400 | abandoned pasture | 33 | 76 | 24 | - | 4 |
| THM 16 | St.-Jeure-d'Ay | 07 | 500 | little grazed plot, loam | 33 | 97 | 3 | - | 9 |
| THM 17 | Luc-en-Diois | 26 | 650 | sheep-grazed, poor in herbs | 33 | - | 100 | - | - |
| THM 18 | Apres | 05 | 750 | orchard-meadow | 33 | - | 100 | - | - |
| THM 19 | La Bâtie-neuve | 05 | 800 | meadow, little manured | 33 | - | 100 | - | - |
| THM 20 | Rourebeau | 05 | 540 | meadow, heavily manured | 33 | - | 100 | - | - |
| THM 21 | Sisteron | 04 | 480 | grassy bank | 33 | - | 100 | - | - |
| THM 22 | La Javie | 04 | 780 | abandoned hay-field | 32 | - | 100 | - | - |
| THM 23 | Riez | 04 | 500 | alfalfa-field, margins | 33 | - | 100 | - | - |
| THM 24 | Reillanne | 04 | 420 | moist grassland | 34 | - | 100 | - | - |
| THM 25 | La Réglisserie | 30 | 70 | sheep-grazed vineyard margin | 30 | - | 100 | - | - |
| THM 26* | St. Jean-du-Gard | 30 | 190 | pasture, little grazed | 24 | 92 | 8 | - | - |
| THM 27 | Aulas | 30 | 400 | orchard meadow | 34 | 76 | 24 | - | 8 |
| THM 28 | Le Vigan | 30 | 370 | mown and trodden public lawn | 23 | 64 | 36 | - | - |
| THM 29 | Col de la Banière | 12 | 800 | meadow | 33 | 46 | 54 | - | - |




meadow with alfalfa
meadow, open stand
alfalfa-field, open stand
ruderal grassland
ploughed hay-field
infrequently mown hay-field
heavily manured pasture
meadow, very rich in herbs
country-lane, -sides
rich pasture
rich pasture
heavily manured hay-field
rich pasture
rich pasture
rich pasture, cattle-damaged
rich pasture, cattle-damaged
rich pasture
little manured, sheep-grazed plot
rich pasture, cattle-damaged
much trodden lawn
manured hay-field
pasture cattle-damaged
ruderal heavily manured pasture
sparingly manured neighbouring plot
rich, heavily manured hay-field
meadow
rich pasture
rich grassland, crop rotation
moist poor Carex-rich hay-field
old pasture, sod locally damaged
little grazed, poor plot
rich pasture, may Tar's, many herbs
as THM 59
as THM 59
poor, heavily grazed, sod damaged
rich pasture, many Tar's




| Sample number | Locality in France | $\begin{aligned} & \text { Dept. }{ }^{1} \\ & \text { no. } \end{aligned}$ | Height <br> m.a.s.l. | Habitat | No. of plants | Pollen diagnosis ploidy-level (\%) |  | $\begin{aligned} & \begin{array}{l} \text { Pollen } \\ >10 \% \end{array} \\ & \hline ? \end{aligned}$ | sterility (2x only) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  | 2x | 3x |  |  |
| THM 63 | bis Contrexéville | 88 | - | rich pasture | 10 | 100 | - | - | - |
| THM 64 | Dombrot-le-sec | 88 | 400 | pasture, many Tar's | 33 | 3 | 97 | - | - |
| THM 65 | Luxeuil-les-Bains | 70 | 350 | pasture, little manured | 33 | 30 | 70 | - | - |
| THM 66 | Remiremont | 88 | 400 | meadow | 33 | - | 100 | - | - |
| THM 67 | Urbės | 68 | 480 | meadow | 10 | 100 | - | - | - |
| THM 68 | Thann | 68 | 410 | heavily manured meadow, many Tar's | 33 | 66 | 34 | - | 30 |
| THM 69 | Lapoutroie | 68 | 360 | meadow | 33 | 100 | - | - | 3 |
| THM 69 | bis Fraize | 88 | - | rich pasture | 10 | 70 | 30 | - | - |
| THM 70 | Rambervillers | 88 | 480 | meadow | 33 | - | 100 | - | - |
| THM 71 | Schirmeck | 67 | 300 | meadow | 33 | 3 | 97 | - | - |
| THM 72 | Abreschviller | 57 | 350 | meadow | 33 | - | 100 | - | - |
| THM 80 | Nanteuil-les-Maux | 60 | - | pasture | 33 | - | 100 | - | - |
| THM 81 | Montereau | 77 | 130 | alfalfa-mixed pasture | 28 | - | 100 | - | - |
| THM 82 | Chevannes | 45 | 120 | little manured pasture | 32 | - | 100 | - | - |
| THM 83* | la Chapelle-sur-Aveyron | 45 | 130 | manured brook meadow | 32 | 25 | 60 | 15 | - |
| THM 84 | St. Amand-en-Puisaye | 58 | 240 | manured pasture | 33 | 24 | 76 | - | 12,5 |
| THM $85 *$ | Baugy | 18 | 170 | horse-grazed pasture | 33 | 39 | 21 | 39 | 7,5 |
| THM 86 | St. Christophe-en-Boucherie | 36 | 230 | pasture | 32 | 3 | 91 | 6 | , |
| THM 87 | Thevet-St. Julien | 36 | 200 | heavily manured pasture | 31 | 74 | 13 | 13 | 4 |
| THM 88 | St. Benoit-du-Sault | 36 | 250 | poor pasture | 33 | - | 100 | - | - |
| THM 89 | Confolens | 87 | - | sheep-grazed rich pasture | 32 | 75 | 19 | 6 | - |
| THM 90 | St. Claud | 16 | - | poor pasture | 33 | 58 | 21 | 21 | - |
| THM 91 | Montmoreau | 16 | 130 | damp meadow, vulgaria A | 25 | 68 | 12 | 20 | - |
|  |  |  |  | palustria $\mathbf{B}$ | 7 | - | 100 | - | - |
| THM 92 | Cognac | 16 | 40 | ploughed, resawn meadow | 6 | 50 | 50 | - | - |
| THM 93 | Tonnay-Boutonne | 17 | 30 | ploughed, resawn meadow | 33 | 97 | 3 | - | - |
| THM 94 | Niort | 79 | 70 | pasture | 33 | 36 | 39 | 24 | - |
| THM 95* | Ste. Hermine | 85 | 40 | pasture | 33 | 100 | - | - | 18 |
| THM 96 | St. Gilles-Croix | 85 | 20 | pasture, sod cattle-damaged | 19 | - | 100 | - | - |





| Sample number | Locality in France | Dept. ${ }^{1}$ no. | Height m.a.s.l. | Habitat | No. of plants | Pollen diagnosis ploidy-level (\%) |  | $\begin{aligned} & \text { Pollen } \\ & >10 \% \end{aligned}$ | sterility <br> ( 2 x only) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  | 2 x | 3x |  |  |
| TGT 3 | Blacons | 26 | 350 | meadow | 33 | - | 100 | - | - |
| TGT 4 | Flaviac | 07 | - | pasture | 30 | - | 100 | _ | - |
| TGT 5 | Fresnau | 26 | - | road-side | 30 | - | 100 | - | - |
| TGT 6 | Col du Devès | 26 | - | - | 33 | 67 | 21 | 12 | - |
| TGT 7 | Plan-de-Baix | 26 | - | pasture | 30 | - | 100 | - - | - |
| TGT 8 | St. Roman | 26 | - | pasture | 33 | - | 100 | - | - |
| TGT 9 | Vercheny | 26 | - | meadow | 32. | - | 100 | - | - |
| TGT 10 | Le Havre | 76 | sea | road-side | 33 | - | 100 | - | - |
| TGT 11 | Le Havre | 76 | sea | pasture | 30 | - | 100 | - | - |
| TGT 12 | Criel-sur-Mer | 76 | sea | Falaise-coast | 33 | - | 100 | - | - |
| TGT 13 | Criel-sur-Mer | 76 | sea | pasture | 33 | - | 100 | _ | - |
| TGT 14 | Blangy-sur-Bresle | 76 | - | clover-field | 33 | - | 100 | _ | - |
| TGT 15 | Halloy/Lucheux | 80 | - | pasture | 33 | 15 | 85 | - | - |
| TGT 17 | Sospel | 06 | 700 | not recorded | 8 | 12 | 24 | 60 | - |
| TRL 1 | Godivelle | 63 | - | little grazed, species rich pasture | 30 | 100 | - | - | - |
| TRL 2 | Espinchal-Egliseneuve | 63 | - | heavily grazed pasture | 33 | 91 | 9 | - | 6 |
| TRL 3 | Lac Pavin | 63 | - | ruderal grassland | 30 | 100 | - | - | - |
| TCH 16 | Oloron-Ste-Marie | 64 | - | not recorded | 20 | - | 90 | 10 | - |
| TCH 17 | Peyrehorade | 40 | - | pasture | 18 | 78 | 22 | - | - |
| TS 1 | Super Lioran | 15 | 1300 | road-side | 33 | 3 | 97 | - | - |
| TS 2 | Super Lioran | 15 | 1500 | forest-margin | 33 | 15 | 73 | 12 | - |
| TS 3 | Super Lioran | 15 | 1500 | heavily grazed mountain meadow | 30 | - | 82 | 18 | - |
| TS 4 | Col de la Fageole | 15 | 1000 | road-side | 25 | 16 | 80 | 4 | - |
| TS 5 | Lempdes | 43 | 400 | meadow camping ground | 27 | 52 | 30 | 19 | 12 |
| TS 6 | Col du Lautaret | 05 | 2058 | road-side | 33 | - | 100 | - | - |
| TS 7 | Villar-d'Arene | 05 | 1650 | road-side | 33 | - | 100 | - | - |


| TS 8 | La Grave | 05 | 1350 | road-bank | 33 | - | 100 | - | - |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| TS 9 | Mont-de-Lans | 38 | 1300 | road-bank | 31 | - | 100 | - | - |
| TS 10 | Les-2-Alpes | 38 | 1650 | pasture | 30 | - | 100 | - | - |
| TDB 1/2 | Bergerac, Dordogne | - | - |  | 2 | 100 | - | - | - |
| TDB 3/4 | Bergerac, Dorgogne | - | - |  | 2 | 100 | - | - | 100 |
| TDB 5/6 | Decize, Nièvre | - | - |  | 2 | 100 | - | - | - |
|  | Locality in Italy La Thuile, Aosta | - | 1440 | road-side | 33 | 18 | 76 | 6 | 14 |
| TS 12 | La Thuile, Aosta | - | 1700 | road-side | 29 | 18 | 100 | 6 | 1 |
| TS 13 | Col Pt. St. Bernard, Aosta | - | 2000 | runderal alpine meadow | 33 | - | 100 | - | - |
| TS 14 | Val di Rhèmes, Aosta | - | 1500 | road-side | 34 | 6 | 94 | - | - |
| TS 15 | Val di Rhèmes, Aosta | - | 1725 | road-side | 33 | 30 | 64 | 6 | - |
| TS 16 | Val di Cogne, Aosta | - | 1400 | road-side | 33 | 6 | 94 | - | - |
| TS 17 | Val di Cogne, Aosta | - | 1540 | ruderal grassland | 32 | - | 100 | - | - |

can be distinguished from polyploid ones. As a consequence of the relative abundancy of the triploid level in the section Taraxacum one may assume that in most cases a non-diploid, thus polyploid diagnosis stands for a triploid individual. Compare table 2 and the above mentioned literature. Some additional remarks to this method are to be given:

- Preferably pollen from still closed florets should be examined because there is always a chance that foreign pollen has previously been deposited on open ones and thus becomes included in the assessment. However, it is not always possible to exclude this source of error in herbarium material, so that analyses of such material need not always be reliable, but one may assume that as a result of such a 'pollination pollution' the diploid scores may be a bit low for the reason that the assessments are conservative.
- The data recorded by Jenniskens et al. (1983) show clearly that regionally a not inconsiderable part of a stand of dandelions may consist of individuals which, although triploid, have a regular of meiosis judging by the low variation of the pollen diameter. Such specimens are placed in table 1 in the column:?, which means diagnosis uncertain.
- Presumably the flowering periods of plants at the diploid level and those of individuals at the triploid one do not strictly coincide. It follows that the precise moment of a single sampling may have some bearing upon the relative abundance of the ploidy levels in the stand sampled (see also Den Nijs \& Sterk 1980).

The last two considerations, also in view of the relatively small sample size (30-35 specimens) render it necessary to accept that the percentages of the ploidy levels per sample, as shown in table 1, are indicative rather than absolute. In a selected number of population samples chromosome counts were carried out in the manner described in previous papers of this series (DEN NiJs et al. 1978, Den Nijs \& Sterk 1980).

## 4. RESULTS

### 4.1. Generalities

Table 1 gives a survey of the larger samples and of their origin, a concise habitat characterisation, and the results of the pollen size analyses. Those populations in which chromosome counts were carried out are indicated with an asterisk.

In 96 out of the 154 analysed samples diploid, sexual individuals were found. Of these 96 the majority was mixed, diploids and triploids being represented in varying ratios: the $2 x$ portion ranges from $3 \%$ to $97 \%$. Only 11 samples seemed to be exclusively diploid. Calculated over all samples the proportion of diploids is a little over $50 \%$. The total number of individually studied specimens was over 4,500 , which number is about 5,500 when the smaller samples and herbarium sheets are included.

Figs. 1-4 show some examples of pollen preparations on which our diagnoses rest.


Figs. 1-4: Some examples of pollen variability upon which the ploidy diagnoses are based.

1. Taraxacum aganophytum v.S.; Verbier, Val de Bagne (CH) 1620 m , BR coll. Lawalrée 22556; Diagnosis: diploid.
2. T. grypolobum Sahlin; Verbier, Val de Bagne (CH) 1600 m , BR coll. Lawalrée 23134; Diagnosis: diploid.
3. T.paramecacrum Sahlin; Savoleyres-Croix-de-Coeur, Val de Bagne(CH) 2200 m , BR coll. Lawalrée 22690; Diagnosis: diploid.
4. T. lacistrum Sahlin; Verbier, Val de Bagne (CH) 1700 m, BR coll. Lawalrée 22534; Diagnosis: triploid.

Figs. 5-6: Examples of chromosome slides:
5. Plant THM 85-1, Baugy, east of Bourges (Dept. Cher): $2 n=16$ ( 15 chr. and a vague dot, representing the 16 th., not in focus).
6. Plant THM 95-1, Ste. -Hermine, between La Rochelle and Nantes (Dept. Vendée): $\mathbf{2 n}=16$, note the very large fragments separated by the secondary constriction (indicated by an arrow).

Table 2: Survey of chromosome counts in 40 plants taken from 11 populations.

| Pop. no. | No. of <br> plants <br> studied | Chromosome number <br> diploid | triploid |
| :--- | :--- | :--- | :--- |
| THM 26 | 1 | $2 n=16$ |  |
| THM 32 | 4 | $2 n=16,16,16$ | $2 n=24$ |
| THM 41 | 1 | $2 n=16$ | $2 n=24,24,24,24$ |
| THM 57 | 4 | $2 n=16,16,16,16,17$ | $2 n=24$ |
| THM 83 | 6 | $2 n=16,16$ |  |
| THM 85 | 2 | $2 n=16,16$ | $2 n=24,24$. |
| THM 95 | 2 | $2 n=16,16,16,16$ | $2 n=24,24,24,24,24$ |
| THM 104 | 2 | $2 n=16,16,16,16$ | $2 n=24$ |
| THM 110 | 9 | $2 n=16,16$ |  |
| THM 111 | 4 |  |  |
| THM 118 | 3 |  |  |

Two points of interest in table 1 are the following:

- Upon the whole the number of dubious cases is very low, i.e., triploids with subregular pollen are relatively rare. Locally they may be of more common occurrence: in the northern part of the area sampled towards the border of the previously determined diploids range (compare also fig. 7).
- Male sterility (i.e., the incidence of pollen without cytoplasm is, generally speaking, rare among diploids, but is found scattered throughout the area.


### 4.2. Chromosome counts

Table 2 shows the results of the chromosome counts as carried out in 11 population samples. The corresponding localities are indicated in fig. 7 by their code number. No deviating counts were found in respect to the diagnoses based on the pollen grain diameters. Figs. 5 and 6 are examples of metaphase plates. In a few individuals (such as THM 83 and 95) a certain degree of internal variation of the number was recorded ( $2 n=17,18,15$ ). An odd specimen had $2 n=$ 17. It is not at all unlikely that such an instability and variation is attributable to the pollination of a diploid mother plant with somewhat irregular pollen from a triploid individual ( $\mathrm{n}=7,9,10$ ). Such a variation may be regarded as indicative of gene-flow between the diploid cytodeme and the triploid one.

### 4.3. Herbarium analyses

4.3.1. Material from France: Van Soest Herbarium (incorporated in L.).

- A group of 9 samples (the TB series), each comprising between 6 and 31 individual specimens, 137 in all, from the Puy-de-Dôme. Of these 9 samples 6 are $100 \%$ diploid, one is mixed, and 2 are completely triploid. These data are entered in fig. 7.
- A collection of small samples (leg. De Bray, series TBD), about 60 in all, each consisting of one or two individual specimens, from various parts of France. Of these 60, 19 (from the Dordogne, the area surrounding Le Hâvre,
and the western Banlieu of Paris) were diploid, and only these 'diploid' locations are included in the records of fig. 7 (as black dots).

Of these two collections a number of sheets (in herb. Van Soest) was identified to the microspecies level, so that in these cases the ploidy level could be related to the systematic status. In the following enumeration Lit (erature) refers to previous counts (e.g., " 24 ") and for the assessment of the ploidy level on the bases of pollen characteristics (e.g., " 3 x ").

Sectio taraxacum Triploid
T. ardisodon Dt.
T. pallidissimum v.S.

TRIPLOID

Le Vesinet, Yvelines, TDB 75.
Chatou, Seine-et-Oise, TDB 48.

### 4.3.2. Vallée de Bagne, Valais, Switzerland, Herbarium BR.

The material comprises 138 specimens, all from the Vallée de Bagne, and named: there are 50 microspecies in 6 sections, among which the type specimens of 8 species. An appreciable part of the specimens appeared to be diploid judging by the pollen diameters. This collection contains 26 representatives of sect. Taraxacum of which 11 are diploid, and 17 of sect. Alpestria of which 3 appeared to be diploid, one of these three being represented at the di- and triploid level; another 2 diploid species are of unknown sectional identity. An enumeration of the localities (sometimes several per microspecies) and the results of the pollen diagnoses follows (the sequential herbarium number added between brackets):

DIPLOID
Sectio taraxacum

| T. aganophytum v.S., | Verbier, $1620 \mathrm{~m}(22.556)$. |
| :--- | :--- |
| T. alatiforme Rail. | Versegères $890 \mathrm{~m}(23.525)$ |

T. alatiforme Rail.,

Versegères, $890 \mathrm{~m}(23.525)$.
T. cataschistum Sahlin, T. erntrum v.S.,
T. fasciatiforme v.S., T. grypolobum Sahlin,
T. infucatulum Sahlin, T. ligerinum Sahlin, T. peliogoniatum Sahlin, T. pulchrifolium Markl., T. olivaceoides v.S.,

## Sectio alpestria

T. centrotum Sahlin,
T. glandolense v.S.,

## Section UNDETERMINED

T. nantuatum Sahlin,
T. paramecacrum Sahlin,
both DIPLOID and TRIPLOID
Sectio taraxacum
T. brevifloroüdes v.S.,

Verbier, $1620 \mathrm{~m}(22.557), 2200 \mathrm{~m}(22.698), 2100 \mathrm{~m}(23.200)$.
Verbier, 1850 m (21.486); Savoleyres-Croix-de-Coeur, 2200-2250 m(22.689, TYPUS).
Croix-de-Coeur-Savoleyres, 2300 m (21675).
Verbier, $1550 \mathrm{~m}(23122$, TYPUS $), 1600 \mathrm{~m}(23133,23134), 1350 \mathrm{~m}$ (23494).

Verbier, 2100 m (23.196, TYPUS).
Verbier, (23.199)
Verbier, 1620 m (22.558, TYPUS).
Verbier, 1700 m (23.139).
Verbier, 2040 m (23.204).

Verbier, 1650 m (23.169, TYPUS), 1700 m (23.144), 2200 m (23.188).

Verbier, 1620 m (22.555); Savoleyres, 2350 m (22.684).

Savoleyres-Croix-de-Coeur, 2200-2250 m (22.685, 22687).
Verbier, 1850 m (21.485); Savoleyres-Croix-de-Coeur, 2200-2250 m(22.690).

## Sectio alpestria

T. albulense v.S., $\quad 2 x$ : Savoleyres-Croix-de-Coeur, 2200-2250 m (22.686);

3x: Verbier, 2200 m (23.189).
TRIPLOID and HIGHER LEVELS (when indicated)
Sectio taraxacum
T. catameristum Sahlin,

Verbier, 2200 m (23.186).
T. davosense v.S.,
T. ekmanii Dt.,
T. hypopolium Sahlin, T. lacistrum Sahlin,
T. laiense v.S.,
T. lasiodasum v.S.,
T. magnodilatatum v.S.,
T. oblongatum Dt.,
T. praterense Sahlin,

Verbier, 1510 m (22.454).
Verbier, $1700 \mathrm{~m}(23.145), 1480 \mathrm{~m}(23.146)$.
Lit.: Richards \& Sell (1976): $2 \mathrm{n}=24$. Den Nus \& Sterk (1982):
$2 \mathrm{n}=24$.
Verbier, 2040 m (23.206, 2 exx.)
4x?: Verbier, 1650-1700 m (22.534);
$3 x$ : Verbier, 1510 m (22.457, TYPUS); not polliniferous: Verbier, 1510 m ( 22.457 , TYPUS). (Two specimens on one sheet)
Mauvoisin, 2050 m (23.318).
Mauvoisin, 2000 m (21.775).
not polliniferous: les Clerondes, 1980 m (21.627).
Verbier, 1350 m (23.505).
Verbier, 2100 m (23.203).
T. subarmatum Hgd., v.S. and Zb., Verbier, $1550 \mathrm{~m}(23.121), 1700 \mathrm{~m}(23.140,23.141)$.
T. subcanillans Sahlin, les Clerondes, 1980 m (21.624).
T. walo-kochii v.S.,

## Sectio ALPESTRIA

T. fontqueri v.S.,
T. ochrospermum v.S.,
T. ooststroomii v.S.,
T. pallidisquameum v.S.,
T. perfissum v.S.,
T. rhaeticum v.S.,
T. rufocarpoides v.S.,
T. simpliciusculum v.S.,
T. strictolobum v.S.,
T. stylosum v.S.,
T. vereinense v.S.,

Section UNDETERMINED
T. thysanodes Sahlin,

## Sectio ALPINA

T. panalpinum v.S.,

Verbier, 2200 m (23.178, 23.181); Boussine 2050 m (23.307); Mauvoisin, 2000 m (21.771). Lit.: Doll (1982): $2 \mathrm{n}=32$.

## Sectio ERYTHROSPERMA

T. aequabile Hagl.
T. lacistophyllum (Dt.) Raunk.,

Boussine, 2050 m (23.314).
les Clerondes, 1980 m (21.620).
Lit.: Richards \& Sell (1976): 2n: 24, 25; Doll (1982): $2 \mathrm{n} \doteq 24$, 25,32 ; Den Nus \& Sterk (1982): $2 \mathrm{n}=24$.
T. purpureomarginatum v.S., Savoleyres-Croix-de Coeur, 2200-2250 m (22.691); Les Verneys, 1100 m (22.531).
Lit.: Richards \& Sell (1976): $2 \mathrm{n}=24$; Doll (1982): $2 \mathrm{n}=32$.
Verbier, 1970 m (21.489).
Lit.: Richards \& Sell (1976): $2 \mathrm{n}=24$; Doll (1982): $2 \mathrm{n}=24$, 25, 48.

Sectio Fontana
T. aurantellum v.S.,
T. binilobatum Sahlin, T. pohlii v.S.,

Mauvoisin, 2050 m (23.315).

Verbier, 2150 m (23.220).
Boussine, 2050 m (23.303); Verbier 2200 m (23.177); Panossière, $1900 \mathrm{~m}(21.751)$.
la Rechouen, 2200 m (21.598).
Mauvoisin, 2000 m (21.774).
Verbier, 1510 m (22.453); not polliniferous!
Verbier, 1780 m (23.216).
not polliniferous: Bonatchesse, 1570 m (23.421).
Lit.: Richards \& Sell (1976): $2 \mathrm{n}=24$.
Verbier, 2200 m (23.180).
Boussine, 2050 m (23.302).
Boussine, 2050 m (23.312).
Verbier, $1650-1700 \mathrm{~m}$ (22.538).
Verbier, 2040 m (23.209), 2200 m (23.185), 4x?: Verbier, 2200 m (23.182).

Verbier, 2040 m (23.205).

Verbier, 1510 m (22.455).
Verbier, $141500 \mathrm{~m}(23.153)$.
Mauvoisin, 200 m (21.778); not polliniferous: Verbier, 2200 m (23.184).

Lit.: Richards \& Sell (1976): $2 \mathrm{n}=32$.



Fig. 7: Distribution of the samples, including the relative frequencies of the ploidy levels. The small symbols (open or black) represent the smaller samples (mainly herbarium material). Populations from which chromosomes are counted, are indicated with their code number. The polyploids as indicated by an open symbol (parts) are most likely triploids.

Sectio Rhodocarpa
T. schroeterianum Hand.-Mazz., Boussine, 2050 m (23.301); la Chaux-les Clerondes, 2200 m (22.701, 22.702); les Ruinette, 2200 m (23.560); not polliniferous: la Chaux-les Clerondes, $2200 \mathrm{~m}(22.703,23.221)$.
Lit:: Richards \& Sell (1976): $2 \mathrm{n}=24$; Doll (1982): $2 \mathrm{n}=24$, 32.
4.4. Geographical distribution and ecological amplitude of the diploid, sexual forms.
In fig. 7 the distribution of the population samples, of the small samples and, in addition, of a number of the herbarium sheets is shown. The relative size of the black segment in the larger symbols (relating to the larger samples) corresponds with the percentage of diploids; the other diploids are indicated by means of black dots. The diploid cytotype is clearly very wide-spread in the area sampled: varying percentages of diploids were encountered in most parts of France visited. Exceptions are for the time being parts of the northern and western regions (Brittany, Normandy, etc.) and a part of the French Alps to the S. of Grenoble. Diploids are particularly common in the area to the S. of the line Le Mans-Strasbourg to become rarer towards the N. A more intensive sampling may show that the percentage of diploids decreases gradually in the populations as we found earlier in Central Germany (Frankfurt-Stuttgart), compare Jenniskens et al. (1983). The most north-westernly localities in the area surrounding le Hâvre (series TDB, see § 4.3) and near Arras (TGT 15) clearly point in that direction, but up to now we have not procured any living plant material from these areas, so that no actual chromosome counts of such advanced locations are available.

Some noteworthy points:

- The presence of diploids to the S. of the main mountain chain of Alps in the Val d'Aosta, Italy (TS 11/16) and in the Vallée de Bagne, Valais, Switzerland (herb. BR).
- The incidence of diploids in northern Spain (not shown in fig. 7) in the area of Picos d'Europa.

The concise habitat indications in table 1 show that the samples were collected in grassland lots with a varying rate of cultural stress, but upon the whole there is no manifest correlation between the nature of the sites and the intensity of the management on the one hand, and the occurrence or absence of diploids on the other, diploids having been found not only in both heavily fertilized, productive pastures with a high grazing stress and urban parks with a very severe mowing regime, but also in poor, unmanured hay fields both in the Jura and the Vosges and the extreme W (Charente, Loire-Atlantique). In the latter region they may grow sympatrically with representatives of sect. Palustria (e.g., THM 91).

The width of the ecological amplitude of the diploid cytotype is alos expressed in a climatological comparison, because it occurs from eu-atlantic lowland conditions in the extreme W to alpine situations in the (high) montane zones (Massif

Central: up to 1500 m ; Val de Bagne: till over 2000 m alt.!).
The geological and edaphic conditions also cover a wide range: granites, eruptive rocks, cretaceous rocks, Tertiary and alluvial deposits, heavy loams and clays but also sandy substrates and stony soils.
More or less in contrast to the broad amplitude, a comparison between the samples THM 52A and 52B indicates that the stands of dandelions in two adjacent fields may contain a widely different percentage of diploid individuals, a much higher rate of disturbance apparently being detrimental to the diploid forms. This shows that a comparative inquiry into the ecology of the di- and the triploid cytotypes was indicated. Such a study, both by means of observations in the field and experimentally, is being undertaken.

## 5. DISCUSSION

### 5.1. The cytogeographical aspects

Owing to the procedure followed during the sampling the recorded percentual distributions of di- and of triploids in a population or stand can only have an indicative rather than an absolute value. The differences in pastural ecology, the relatively small sample size, and the one-time gathering are the uncertain


Fig. 8: Map showing the original (indigenous) part of the distribution area of the section Taraxacum (after Doll 1982). The "diploid" areas and, as far as known, isolated locations are indicated. According to the present authors diploids may well be present in the dotted regions.
factors involved, as pointed out before (Den NiJS \& Sterk 1980).
In contrast to the situation in Bavaria (Jenniskens et al. 1983), in the present study only a few triploid specimens were found in the category of doubtful cases (pollen type PT as in Sterk et al. 1982). The diagnoses based on the examination of pollen alone were consistently confirmed by subsequent chromosome counts. The quick routine method once more proved to be convenient and useful.

When the hitherto recorded distribution of sexual and diploid forms of sect. Taraxacum in the G.F.R. and the Alpine region (Fürnkranz 1966, Den NiJs \& Sterk 1980, Jenniskens et al. 1983) and in the most southern part of the Netherlands (STERK et al. 1982) is related to the present survey in France, the following deductions come to mind (compare also fig. 8):

In a considerable part of the geographical range of sect. Taraxacum (as indicated by Doll 1982) secondary diploid (and sexual) forms are found. The present data suggest the incidence of diploids outside the area sampled by us in northern France and in Belgium, thus linking up with the Dutch localities and the adjacent area of Germany. (Den Niss, in prep.). The very scattered occurrence of diploids in county Durham (England), see Richards (1968), may indicate that in at least SW England also diploids may be expected to occur.

The range of sect. Taraxacum also extends into the Iberian Peninsula, Italy and the Balkans. From Spain no other records are known apart from that from Picos d'Europa. The diploids found there clearly indicate that the Pyrenees do not form the southwestern limit of the range of the diploid forms, so that further investigation is indicated.

The same holds for Italy: the diploids are now known to occur in the southern Alps (Aosta region and also Valais, Switzerland) and in the southern Tyrole near Trento (Den Niss, unpublished data), so that the mountain chains of the Alps do not constitute a barrier either against a farther N-S distribution - this in contrast to the supposition made by SAHLIN (1982) who expressed as his expectation that diploids did not cross the Alpine chains.

As regards south-eastern Europe, only sporadic data are available. In view of the presence of diploid taxa of sects. Taraxacum and Erythrosperma in the eastern Alps, the Vienna Basin and the adjoining part of Slovakia (Fürnkranz 1966; Richards 1970; Den Nijs \& Sterk 1980; Jenniskens et al. 1983) and in southern Europe (Doll 1972) one may anticipate the incidence of diploidy in Taraxacum in other parts of Czechoslovakia and the Balkans (and in S. Europe in general). The floras of the eastern escarpement of the Alps, Slovakia, the Vienna Basin and the surrounding, relatively warm and dry areas contain many more or less xerothermic taxa as a pannonic phytogeographical element whose main centre of distribution lies farther towards the S-E Balkans and Asia Minor (compare, e.g., Niklfeld 1973; Den NiJS 1983). A relevant cytogeographical study is intended.

The survey map of fig. 8 shows a clear disjunction between the Eastern and the Western parts of the range of the diploids (compare also Jenniskens et al. 1983). There is an extensive western part-range of the diploids of sect. Taraxacum proper and a still in size incompletely known eastern one of the pannonic
vicariant of this section (Sahlin 1972, 1979). This situation suggests a correlation with the Pleistocene glacials and the associated western and eastern refugia (or centres of migration, respectively).

The incidence of secondarily originated diploid forms is not restricted to sect. Taraxacum. In the area so far studied, also diploid Alpestria taxa have been encountered, and some diploids with Palustria characteristics have also been recorded. Elsewhere in Europe diploid forms of sect. Erythrosperma have been found: the eastern Alpine escarpment (see above), Durham (England): T. brachyglossum (Richards 1968) and S. Europe (Doll 1972). In Asia, especially in Japan, diploids are also of wide-spread incidence in the sects. Ceratophora and Mongolica (Morita 1976, 1980). Seventeen species from several hundreds of localities are involved. Such findings suggest that rediploidisation has occurred on a large scale in several divergently advanced sections of the genus Taraxacum as a parallism. Diploid-polyploid cycles as mechanisms of evolutionary progression have also been noted in other taxa: De Wet (1971, 1980): Dichanthium and Botriochloa; Ehrendorfer (1963): Calamagrostis. Stebbins (1980), on the other hand, considers this strategy to be of only minor significance. Pertaining experimental investigations in Taraxacum are in progress; the preliminary results of these studies render it highly probable that reduced pollen from triploid individuals as obviously formed in various quantities may fertilize haploid egg cells of diploid plants, so that no diploid male parents are required to produce an offspring of isolated diploid plant. Viability being disregarded as a complicating factor, the population density of the diploid forms may thus increase irrespective of the number of diploids already present in the population (Sterk \& Den Niss, in prep.).

The biological background of this process, which is most probably demo-graphic-genetically and demographic-ecologically very complex, is as yet still obscure. It may signify that the sexual (and diploid) system of reproduction and the agamospermous (and triploid) one are directly opposed. Both systems have their pros and cons (compare Maynard Smith 1979). Summarizing some of these points: sexual: development of new genotypes with adaptational advantages; capability to occupy new niches; risk of loss of individuals by insufficient immediate fitness. Asexual: immediate fitness maintained through the absence of recombinations; seed-set independent of pollinations; as a consequence of the small number of genotypes no rapid adaptational changes which cause problems in changing environments. The two modes of reproduction are presumably not in constant confrontation, however, but rather constitute a complementary adaptive system which results from gene flow between the diploid and the triploid levels. It would seem as if in southwestern and Central Europe there is (or was) a shift towards the sexual form of reproduction, apparently by rediploidisation.

For various but mainly practical reasons, in the majority of the samples neither any attention was paid to the morphological variation nor to the taxonomical aspects. The great ecological diversity of the sites where diploids and triploids appear to grow suggests that within the established range of habitats from the
sea level to the alpine zone, and in diverse climatological and edaphic situations, a gamut of ecotypes is present. Also in view of the opulence of micro-species in pastures, e.g., in The Netherlands (STERK et al. 1983) and in Austria (FÜRNKRANZ 1966), and of the great morphological divergence in the grasslands under investigation, one may expect that many of these microspecies are diploid or partly so. The collection of named taxa included in the present study provides some insight into the systematic aspects of the present findings.

### 5.2. Taxonomic aspects

In all, diploid individuals have been recorded in 28 named taxa of which 3 belong to sect. Alpestria and 23 to sect. Taraxacum. A number of microspecies contain both cytotypes: T. albulense, T. aurosulum, T. polyodon, and T. brevifloroides. Such taxa are cogent proof of the very close relationship between the cytotypes, in fact so much so that experienced taraxacologists cannot distinguish between them. Either an autoploid origin of the triploids or an auto-rediploidisation must be accepted as the most probable.

The records in Van Soest's Taraxacum flora of Switzerland (1969), viz., some 160 microspecies (in sect. Taraxacum and in sect. Alpestria) and some recent additions ( 11 in sect. Taraxacum and 2 in sect. Alpestria) by Sahlin (1982) strongly suggest that many more species may prove to be diploid and more taxa may consist of plants of both the 2 x and the 3 x level. A number of taxa reported now as to be diploid have been said both to produce pollen and to be apolliniferous. Absence of pollen in a dandelion usually means that the plant in question is a triploid one. A number of species is reported in the diagnosis to be apollineferous (Sahlin 1982), but we did find pollen in the type specimens (!) which pollen moreover, led to a diagnosis as a dipliod. The descriptions of such taxa (here T. centrotum, T. cataschistum, T. grypolobum, T. infucatulum, T. peliogonatum) are, therefore, incomplete. If indeed also specimens of these taxa without pollen occur, it follows that these microspecies consist of forms with different ploidy levels.

The diploid taxa have a variety of distribution ranges: some are endemic or have so far only been recorded from a single Swiss canton: T. aganophvtum, T. cataschistum, T. erntrum and T. grypolobum. Other ones are more widespread: T. albulense, T. brevifloroides (the Alps), T. ligerinum (France, Switzerland, Denmark), T.olivaceoides (France, Switzerland), T. pallescens, T. polyodon (western and northern Europe).

These records clearly indicate the appreciable involvement of diploidy and associated problems of hybridisation and gene flow in the formal taxonomy of the genus.

Hybridisation experiments carried out within the scope of the present study (Jenniskens, in prepar.) have shown that diploid specimens hailing from the most diverse habitats and from all parts of the area of distribution can be crossed without a genetical barrier and produce viable and fully fertile progenies.

One must accept that the postulated hybrid swarms (Den Niss \& Sterk 1980 and SaHLIN 1982) may occur all over the range of the diploids. The applicability
of the current micro-systematics to forms from that area may be queried to a progressive degree. It is highly probable that the section Taraxacum, and conceivably (parts of) other sections, are in such a dynamic state of microevolution and speciation that the production of a formal taxonomy is in fact impossible in large parts of the area of distribution (this agrees with views expressed by Doll 1982).

On the basis of the present data and records we can visualize the following picture: In western Europe an extensive and intricate complex occurs of sexual diploid and agamospermous triploid forms (biotypes) of sect. Taraxacum. Between these types gene flow is possible and presumably of frequent occurrence. Taxonomically this complex as a whole could better be treated as a large and very intricate species. In the northern direction the agamospermous mode of reproduction progressively becomes dominant ultimately to become exclusively agamospermous, so that genetically isolated microspecies differentiated which became adapted to certain special microhabitats. It is to be expected that in central (and South-Eastern?) Europe a similar situation exists, that also the sections Erythrosperma and Alpestria are involved in this evolutionary trend, and that also in South-east Asia a similar complicated situation is likely to be present in sections Ceratophora and Mongolica.

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