The biosystemattics of taraxacum

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THE BIOSYSTEMATICS OF TARAXACUM

Being a thesis for the degree of

Doctor of Philosophy at the University of Durham

by

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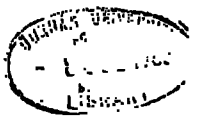

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I would like to thank Mrs. G. Haydon for her very accurate and rapid typing of this thesis.

'I hope in the days to come future thinkers will unlearn us, and find ideas infinitely better - let us get a little alchemy out of the Dandelions!!'

Richard Jefferies, Nature and books.

So now our glasses we'll combine
To fill with Dandelion wine
And toast thy onward way.
May time enrich thy fruitful mind
With health and happiness to find
New species every day.

Lines to Dr. G.C. Druce on finding two new species of Taraxacum to Science. Neither species is now recognised.

R.A.R. Bennett, Oxford Times, 18.3.1926.

Notes on presentation

1. No authorities for scientific names are quoted in the text. A list of all scientific names used, with authorities and references appears as an appendix.

2. All references to scientific works appear fully quoted as another appendix. In the text the author and the date of publication are given.

~~3. All photographs appear as another appendix.~~

4. All species names quoted are 'microspecies' unless otherwise stated. When the term 'species' is used, this refers to microspecies. The aggregate species used by Handel-Mazzetti are termed macrospecies.

5. Sectional taxa are extensively used in the text. These are underlined, and are preceded by the definite article, but are not preceded by 'T'. Genera are not preceded by the definite article. E.G. species: T.norstedtii; section: the Spectabilia; genus Hieracium.

6. A Taraxacum cypsela is here termed 'achene' in deference to general usage. This does not include the projection of the achene joining the achene and the rostrum, which is called the 'cone'. The rostrum connects the achene and the pappus, and is often called the 'beak'. The exterior and interior phyllaries are called 'bracts'. The appendages to these bracts are terms 'cornae' or 'corniculae' depending upon their size. The term 'coloured' means "with anthocyanin pigments".

7. All herbarium sheets of vouchers are deposited at the Fielding-Druce herbarium, Oxford (OXF.) Permanent slides are in the same institution. Exsiccatae will be deposited at a number of other herbaria.

CONTENTS

Chapter 1

AN INTRODUCTION TO THE GENUS

Taraxacum is a large genus in the family Compositae. In this family, it is placed in the sub-family Cichorioidae, and the tribe Cichorieae, and it shares with the other members of this tribe hemaphrodite florets, anthers which are acute at the base, long style arms, which are stigmatic above and become coiled after anthesis, thus achieving automatic self-pollination, and a pappus of hairs.

The genus Taraxacum is diagnosed by its leaves, which are confined to a basal rosette; simple, hollow, lacteate scapes; a naked receptacle, and an achene bearing a (usually) long rostrum (= beak) with a pappus of simple hairs, which is usually white.

The genus is one of unusually wide distribution, although this is thought to be due to efficient dispersal and success in many environments, rather than a reflection of its age. Indeed there is not a little evidence that the genus as we know it is of relatively recent origin (see Chapter 12). Taraxaca are found throughout Eurasia, from Ireland in the West to Kamtchatka in the east, to Syria, Northern India and Korea in the south and to the limit of vegetation in the north. They are found in the continent of America from Greenland and the Aleutian Islands in the north, sparingly down the Rocky Mountains to Mexico, and again at the tip of South America (also in the Andes?). They are also found sparingly in New Zealand, Australia, and the Falkland Islands. In Africa they occur along the Mediterranean coast, as far south as the Atlas Mountains. They thus occur native in all five continents, and

both Polar regions, and in those parts of the world in which they are not found native (S. Asia, and most of America and Africa) they have become widespread immigrants through the agency of man.

The genus has been subdivided into 33 sections. These are summarised in table 1.

Table 1. The sections of Taraxacum

Section	Distribution	Habitat.	Breeding behaviour
Glaciala	Italy, ? Greece	Xerophile	-
Rhodotricha	W. and C. Asia	Xerophile	Sexual. Self-incompatible
Oligantha	W. Asia	Xerophile	Sexual. Self-incompatible
Leucantha	W. Asia	Xerophile	Sexual. Self-incompatible
Orientalia	W. and C. Asia	Helophile	Sexual. Self-incompatible
Leptocephala	S. Europe	Helophile	Sexual. Self-compatible
Serotina	S. Europe	Xerophile	Sexual. Self-compatible
Macrocornuta	W. Asia, N. Africa	Xerophile	Sexual. Self-incompatible
Scariosa	S. Europe	Xerophile	Sexual. Self-incompatible
Kashmirana	C. Asia	-	Sexual. Agamospermic
Tibetana	C. Asia	-	Sexual. Agamospermic
Mongolica	E. Asia	-	Sexual. Agamospermic
Coronata	E. Asia	-	-
Calanthoidia.	E. Asia	-	-
Sinensia	E. Asia	-	Agamospermic
Laevia	Circum-polar, Mountains of Europe, Antarctica	Tundra	Sexual. Agamospermic
Obovata	W. Mediterranean	Xerophile	Agamospermic
Porphyrantha	W. Asia (U.R.S.S.)	-	Agamospermic
Spuria	W. Asia	Xerophile	Agamospermic
Ceratophora	Circum-polar, Mountains of America and Europe,	Rock-ledges	Agamospermic
Montana.	Alps, Carpathians	Wet places on Mountains	Agamospermic (one sexual sp.)

Table 1 (cont.)

Section	Distribution	Habitat.	Breeding behaviour
Alpina	Alps, Pyrenees, Carpathians.	Mountain grassland	Agamospermic
Cucullata	Alps (? Corsica)	-	-
Dissecta	Alps	-	-
Parvula	Himalayas	-	-
Obliqua	W. Europe	Dune-slacks	Agamospermic
Rhodocarpa	Alps	-	Agamospermic
Eu-Erythrocarpa	E. Europe, W. and C. Asia	-	Agamospermic (One sexual sp.)
Erythrosperma.	Europe, W. Asia. America (introd.)	Xerophile	Agamospermic, some facultative and sexual. Self-incompatible
Palustria	Europe, W. Asia	Helophile	Agamospermic
Spectabilia	N.W. Europe, Greenland	Wet places	Agamospermic
Boreigena	N. Scandinavia	Birch-Tundra	Agamospermic
Alpestria	Alps	-	-
Vulgaria	World-wide (native in Europe)	Open ground, grassland	Agamospermic, some facultative and sexual. Self-incompatible.

The diagnostic feature of each section are summarised in table 2.

Table 2. Diagnostic characters in the Taraxacum sections

Section	Size, stature	Scape	Exterior bract.	Fl. diam.	Achene colour.	Rostrum.	Pappus
Glacialia	Small, Adp.	Many, thin	Linear, erect	10–15 mm.	Grey	0	Brown
Rhodotricha	Medium. Adp. narrow, fleshy	"	" , scarious margined	15–25 mm.	Brown	Shorter than achene	Pale reddish
Oligantha	Medium, leathery, few prickly, Adp.		Linear, stiff glaucous	30 mm.	Brown	Shorter than achene	Off-white
Leucantha	"	–	–	40, white	Grey, long	"	"
Orientalia	Small, erect	–	Erect, black white margined	15–30 mm.	–	Equals achene, thick	"
Leptocephala	Medium, adp. narrow, fleshy	Many. thin	"	"	Grey	"	Pale brown
Serotina	Medium, leathery ovate, tomentose	–	Erect, narrow, brown, thin.	40 mm.	Grey–brown long	Exceeding achene, narrow	White
Macrocornuta	Medium, ± fleshy	–	Erect, broader, cornate	35 mm.	Brown small	"	"
Scariosa	Medium, adp.	–	Ovate, adp. scarious margined	30 mm.	Brown small	"	"
Kashmirana	Small, erect	thin	Spreading	25 mm.	"	"	"
Tibetana	Stout, adp.	–	"	40 mm.	"	"	"

Table 2 (cont.)

Section	Size, stature	Scape	Exterior bract.	Fl. diam.	Achene colour	Rostrum	Pappus
Mongolica	Stout, adp.	–	Ovate, cornate	50 mm.	Straw, medium	Exceeding achene, narrow	White
Coronata	"	–	"	"	" in a 'crown' above	"	"
Calanthoidia	"	–	Ovate, adp, cornate	"	Straw, large	"	"
Sinensia	"	–	Ovate, adp.	"	"	"	"
Laevia	Erect. slender	Thin	" very dark	20 mm.	Dark, long cone	"	"
Obovata	Medium, erect, ovate, entire, lvs. thin	Thin	Ovate, adp.	45 mm.	Dark, very spiny	Thin, exceeding achene	White
Porphyrantha	Fleshy	–	"	40 mm. purple	–	"	"
Spuria	Erect, fleshy	Thick, wooly 1-3 fl.heads	"	50-70 mm.	Straw, very long	"	"
Ceratophora	Erect, medium	Thick, long	Erect, cornate	50 mm.	Straw, rather small	"	"
Fontana	Erect, lvs. and petioles wide	"	Erect, ovate lanceolate	45 mm.	Brown, rather small	"	"

Table 2 cont..

Section	Size, stature	Scape	Exterior bract.	Fl. diam.	Achene colour	Rostrum	Pappus
Alpina	Small, adp.	Short, thin	Erect, ovate lanceolate	30 mm.	Brown, rather small	Shorter	White
Cucullata	Erect, medium	Thick, long	"	50 mm. ligules squarrose, narrow ochraceous	"	Long	"
Dissecta	Very many lvs., adp. highly dissected	Very many, thin	"	25 mm.	"	"	"
Parvula	Very many lvs. adp. less dissected	"	"	15-20 mm.	"	"	"
Obliqua	Adp. fewer lvs. highly dissected	-	" corniculate	35 mm.	"	"	"
Rhodocarpa	Adp.	-	Ovate, adp. white margined	35 mm.	Red, rather small	"	"
Eu-erythrocarpa	Erect	-	Usually corniculate	40-50 mm.	Red, rather long, long cylindrical cone	"	"
Erythrosperma	Lvs, dissected	Thin	"	20-35 mm.	" smaller	"	"
Palustria	Erect, lvs. linear	-	Ovate, adp., wide margined	20-40	-	"	"

Table 2 (cont.)

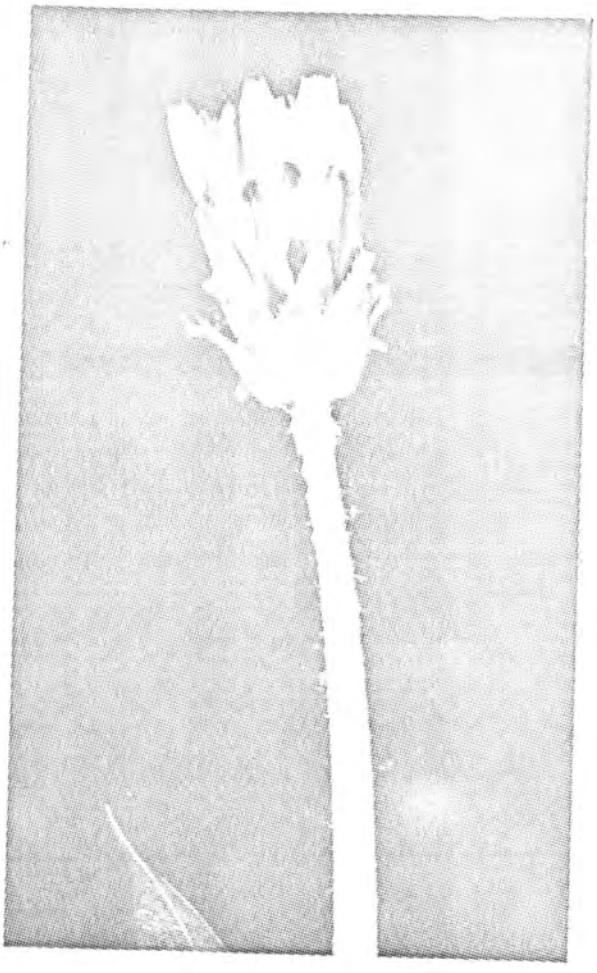
Section	Size, stature	Scape	Exterior bract.	Fl. diam.	Achene colour	Rostrum	Pappus
Spectabilia	-	-	Ovate-lanceolate, narrow margined	30-60 mm.	Pale, rather long		White
Boreigena	Medium, erect	Medium	Erect, ovate-lanceolate	50 mm.	Small, brown	Thin, exceeding achene	"
Alpestria	"	"	Erect, very dark, suffused purple	40 mm.	Medium, reddish	"	"
Vulgaria	-	-	Linear-lanceolate, usually reflexed	30-70 mm.	Small, brownish	"	"

Notes. These few characters are important in the sectional taxonomy of Taraxacum, but it will be seen that not only these characters can be used for sectional determination. An experienced taxonomist will be able to place a specimen in a section with little difficulty, although many sections overlap in a few characteristics. The purpose of this table is merely to give some account of the range of variation in the genus, and to give the reader some idea of the appearance of the sections when they are mentioned in the text.

As might be expected in such a widespread and numerous genus, a large number of species have been described. Indeed with around 2000 species, this ranks among the largest genera known. Only 100-150 of these species are amphimictic, however, it having been established for over 50 years that many Taraxaca are obligately agamospermous. More recent research has shown that this agamospermy is invariably associated with polyploidy; that it is usually obligate; that it is a form of agamospermy known as semi-heterotypic diplospory; and that it occurs in all but a few sections of the genus, and throughout the range of the genus.

The chromosomes of Taraxacum are small, meta-, or sub-metacentric, and vary from 1.8 to 4 microns in length when fully contracted at metaphase. The base-number of chromosomes in the genus seems to be always $x = 8$. Some chromosomes have rather large satellites, and small supernumerary chromosomes are not infrequent. In the apomictic species many cytological abnormalities such as aneuploidy, and aneuploid chimaeras, polyploidy and polyploid chimaeras and in meiosis, many types of associations, very uneven segregation, and occasionally, interchanges are found. Even in sexual species, Małecka (1962, 1965) has shown the pollen meiosis to be very irregular.

Taraxacum has a number of economic uses. Perhaps the most spectacular of these is the production of rubber from the latex. Apparently most, if not all Taraxaca possess a latex from which rubber can be extracted. During the 1939-1945 war, when rubber was very scarce in the Soviet Union, intensive research was carried out in this country on the rubber-bearing qualities of various species, and it was discovered



Photograph 1. Herbarium specimen of Taraxacum kok-saghyz, grown in cultivation

x 1/4

Photograph 2. Taraxacum kok-saghyz. This photograph demonstrates the character of corniculae on the bracts.

x 1

that a recently collected species from W. Siberia, T.kok-saghyz (photograph 1) belonging to the Macrocornuta, bore up to 90% rubber in its latex. This species was improved by artificially doubling its chromosomes with colchicine and crossing this polyploid with plants from the Vulgaria. A triploid apomict finally resulted (T.kok-saghyz is a diploid sexual) with vigour, larger growth, and of course, unfailing seed formation. This agamospermic hybrid (usually referred to as 'T.kok-saghyz' in the literature), is reputed to have accounted for as much as 60% of the rubber needs of the Soviet Union during this war.

Other, more familiar uses include the old-established custom of using it as a (very effective) diuretic; from this property the dialect name of 'Piss-the-beds' (Scotland and N-E. England) and the French 'Pissenlit' presumably originate. Taraxaca are also used in salads in several countries, and various alcoholic and non-alcoholic beverages, both hot and cold are made from the leaves.

To off-set these useful qualities, the Vulgaria in particular are vigorous and pestilential weeds. The only sure way by which they can be eradicated is through the use of a general weed-killer, or a hormone weed-killer such as 2-4 dichlorophenoxyacetic acid.

Despite the obscure and complicated taxonomy, Taraxaca can be used as useful indicator species in the fields of phytosociology (as in the majority of Scandinavian papers in this subject), phytogeography (as in Böcher, 1938, 1952, Wendelbo, 1959, 1964) and plant history. In the last field, I have undertaken the determination of subfossil achenes from interglacial and full glacial deposits from S. England, supplied by the

Sub-Department of Quaternary Ecology at the University of Cambridge. Several interesting results have ensued including the discovery of seeds belonging to the section Erythrosperma in an interglacial site containing the remains of other thermophilous plants, and the discovery of seeds of the Alpina at the Full-Glacial bed at Nazeing. The latter record is of particular interest as these plants are not now known from Britain.

In the fields of genetics and cytology, Taraxacum has many interesting properties. Perhaps the most fascinating of these is the occurence of diploid sexual and triploid apomictic plants of the same species in the same population in a polymorphic relationship, a hitherto undescribed phenonomon which can lead to interesting conjectures on the origin of apomixis in this group. The great plasticity of the Vulgaria in particular makes them very suitable material for the study of environmental variation. The production of genetically identical seed in the apomicts makes them very useful for this type of study, and in the study of genetic and cytological abnormalities as Sörensen and Guðjónsson have so elegantly demonstrated.

One may conclude by stating that there are many cogent reasons why a satisfactory taxonomy is long overdue in Taraxacum. The macrospecies are heterogeneous, poorly typified, ambiguous, and by far too great in scope to be of much use. The microspecies are beset by synonymy, bad taxonomy, and the ramifications of a very extensive literature without geographic or taxonomic monographing (with the notable exception of Van Soest's recent work, which, as yet, covers only a minute proportion of the genus). At the moment the majority of non-specialist workers use the

macrospecies described in Handel-Mazzetti monograph of the genus (1907). This is so much out of date as to be valueless. In Scandinavia, where the majority of workers in the genus have lived, the literature is not too inaccessible, and is in the native tongue of the land. Many people have become proficient in identifying Taraxaca in these countries, and the plant sciences of these areas are subsequently richer for the knowledge of the local Taraxacum-floras. Scandinavia has a huge Taraxacum-flora (perhaps as a result of this interest), but this, and the very large synonymy, ably handled in Hylander (1941) in which no less than 71 synonyms in the Scandinavian flora alone are quoted have not deterred taxonomists in these countries. I see no reason why a microspecies classification in Taraxacum, condensed into regional monographs, and with the degree of 'splitting' modified in some instances should not become equally acceptable in the rest of the world. The Botany of these areas would certainly gain from it.

Chapter 2

AN INTRODUCTION TO PROBLEMS IN TARAXACUM

It is well-known that apomictic genera such as Taraxacum pose some difficult problems for the taxonomist. As there is little sexuality through the majority of the genus, each individual becomes a 'gene-pool' to itself. Every line of descent is reproductively isolated, and may through somatic mutation, occasional outbreeding, or possibly position effect (Gustafsson 1934b), evolve into distinct, taxonomically recognisable segregates. In theory every line of descent is an evolutionary unit. In practice a discrete number of species are recognised, many of them of a very wide distribution. In fact the geographical and morphological grade of the apomictic microspecies is rather similar to that of amphimictic species in this and other genera. It is clear that during the evolutionary history of Taraxacum some segregates have proved to be more successful than others and these have been perpetuated over a wide area to the exclusion of other less successful genotypes. Thus some species of a very restricted distribution may be of a recent origin, while the majority are of some age and have spread to the limit of their genetic capabilities.

In some areas, and in some sections, the position is not so simple however. In the Vulgaria a large number of relatively little differentiated species can be described, and the scale of the resultant taxonomy is such to deter all but the keenest specialist (in the Scandinavian Vulgaria in particular this is true, and also in the

Icelandic Spectabilia and the Japanese-Mongolica and Ceratophora. The Ceratophora are also very highly differentiated in Greenland). The position is made worse by the lack of regional or sectional monographs in Taraxacum. The large apomictic genera are usually scantily treated in Floras, necessarily so for considerations of space. A notable exception to this is Schischkin's treatment of Taraxacum in the 'Flora of the U.R.S.S.'.

Most apomictic groups do have their specialists however, who will name without hesitation the majority of material. Taraxacum too has had its specialists; the Scandinavians Dahlstedt, Haglund, Lindberg, Marklund, Christiansen, Saarsoo and Railonsala. All except Railonsala are now dead however. There remains only one other authority in the genus, van Soest, of the Hague, who is covering much wider areas of the genus's distribution than most of the earlier workers.

All Taraxacum specialists have shared a common inability to name a percentage of the material that they examined. This has been particularly so in the Vulgaria, Spectabilia, Ceratophora and Mongolica. Other sections such as the Palustria and the Erythosperma are very much easier providing the material is good. This uncertainty over the Vulgaria in particular has given rise to many doubts about the validity of Taraxacum species over the genus as a whole, which in the majority of sections is totally undeserved. It has also engendered a quantity of synonymy; some of it, I suspect, yet to be discovered. There seems little doubt that the confusion reigning in these groups is, in part at last, a reflection

of biological phenomena. The Vulgaria , which are better known biologically than other groups can be shown to be unusually plastic organisms (Chapter 3), and some of the species in this section may be merely variations due to environmental effect.

Sörensen and Gudjonsson have shown in a remarkable series of experiments (1946, 1958), that several species in the Vulgaria are liable to variation in chromosome number, and that each of eight possible monosomic aberrants from a triploid are independently recognisable. These aberrants have been recognised in the field (Borgvall and Haglund, 1958) but may nevertheless be responsible for some specific epithets. Gigas aberrants (2n = 48) and diploids arising from triploid apomicts have also been given specific epithets. Most important of the experimental evidence resulting from work on the Vulgaria has been the demonstration of two separate mechanisms by which polyploid apomictic Taraxaca may become sexual. Sorensen (1958) has shown that certain of the triploid monosomic aberrants are capable of a limited sexuality, although apparently at a very low frequency. More recently Tschermak-Woess (1949) and Fürnkranz (1960) have demonstrated that diploid sexual Taraxaca, apparently in no less than 3 sections, occur at high rates in Austrian populations. These have been shown to form hybrids through pollination by diploid or polyploid individuals of the same or different macrospecies (Fürnkranz unfortunately works by the old classification of Handel-Mazzetti), and it is clear that considerable taxonomic confusion would result from the examination of such a series of hybrids.

In view of the fact that it is possible to obtain sexual individuals in

a number of sections of the genus, it seemed likely that breeding experiments between various species might establish relationships between the different sections. A number of southern European and Asiatic sections, including sexual species, had rarely, if ever, been grown in cultivation and breeding experiments have only once been reported (Poddubnaja-Arnoldi, 1939). In view of the fact that the majority of the genus is agamospermic, these experiments promised to be interesting, as breeding barriers might be less extreme than one would expect in a predominantly amphictic group.

The problem of the very large number of species in Taraxacum and the lack of any co-ordination in the literature is not entirely an academic one. The Flora Europaea treatment of Taraxacum is due in 1970, and as a full account cannot be given there through considerations of space, a need has arisen for a modern macrospecies treatment to supersede that of Handel-Mazzetti. It was thought that some interesting insight into the problem of delimiting the macrospecies might be gained through the use of Numerical Taxonomy.

In conclusion, when I first started to work on Taraxacum it seemed to me that a number of problems bore the hallmarks of possible research topics, namely that the techniques of investigation were reasonably practicable, and it was possible to envisage a useful answer arising from the questions that I was asking. I was unsure which of the topics would prove to be the most useful and fruitful, so I started on a number of promising lines of research. These were designed to answer the following questions which were those which seemed most pertinent at the time.

1. Are existing specific limits seriously blurred by hybridisation?

2. Are existing specific limits seriously blurred by environmental plasticity?

3. Is there a method by which an artificial taxonomic grouping can be arrived at, should the existing taxonomy prove to be mostly unusable?

4. Is it possible to draw tentative conclusions of evolutionary (phyletic) relationships in the genus through breeding experiments and other biological characteristics?

5. What is the situation in the central European populations in which both sexual and apomictic plants occur together? Are both types in the same species? Is there genetic interchange between the two types? Are sexual plants found elsewhere in Europe (i.e. Britain) and if so, are they of an ancestral type, or of a secondary origin?

And over and above these questions lay the personal problem of mastering the taxonomy of this difficult genus.

Chapter 3

ENVIRONMENTAL VARIATION AND GROWTH EXPERIMENTS

Growth conditions

At the outset of my work, I decided that all plants cultivated should be grown in a standard and regulated manner. As material collected as living plants would have been subject to environmental influence before collection, I determined to attempt to grow all the experimental samples from achenes. I found that achenes from all species tried germinated readily on wet filter paper or seed-test paper in Petri Dishes. Germination was usually between 70 and 100% successful, and was completed in 2-6 days (see germination graphs). Surprisingly, these results contrasted with those of Mrs. Hoy-Liu (1963) using the same technique who found that a wide range of species required 5-24 days for germination, and that only 50-70% germination was recorded in most samples. Nearly all my achenes were sown within a year of collection, and results obtained from a few older samples produced results more comparable with those of Mrs. Hoy-Liu. I have had one achene germinate after 4 years, but none after 5 or more years, and germination after 3 years is usually very poor.

Failure of germination has been gratifyingly slight - only 1% of all samples have entirely failed, and these have been either over three years old, or immature. Poor germination has sometimes resulted from fungal infection. This can be prevented with the use of scrupulously clean Petri Dishes, and by keeping the filter paper very wet.

About a week after germination, usually just after the separation of the cotyledons, seedlings were transplanted into plastic soil trays with individual compartments some 3 cm. in diameter and deep. All soil used at all stages has been John Innes No. 3 compost. It was at this stage that 'thinning out' was performed. The selected plants were then grown in the trays for approximately a month until 4-5 rosette leaves had established. They were then transplanted again into 4 inch diameter plastic pots. Initially 3 inch clay pots were used, but were found to be highly unsatisfactory, as they limited growth excessively, and, due to their clay structure, were heavy, difficult to wash, and liable to fracture during hard weather. The 4 inch plastic pots proved admirable in all ways, and appeared to provide sufficient space and nourishment for even the largest species until after the first flowering. If the plant was required after this (which was not often) repotting was advisable. Larger pots were not used through consideration of space and expense. Flowering occurred from $3\frac{1}{2}$ months to 6 months after germination, except for the Mediterranean sections Serotina and Leptocephala, which require vernalisation, and the Spectabilis, which rarely flower freely until the second year leaves have been established (except for T. norstedtii).

All plants were grown in a greenhouse with artificial heat and light. An attempt was made to keep the greenhouse at between 60 and 70 degrees Fahrenheit, and this was largely successful. Light was provided by 6 Phillips 400 watt Mercury Vapour bulbs and greenhouse units. The pots were placed about 6 feet from these on a gravel bench and were lit for 12 hours out of 24. This approximates to the day-length required for

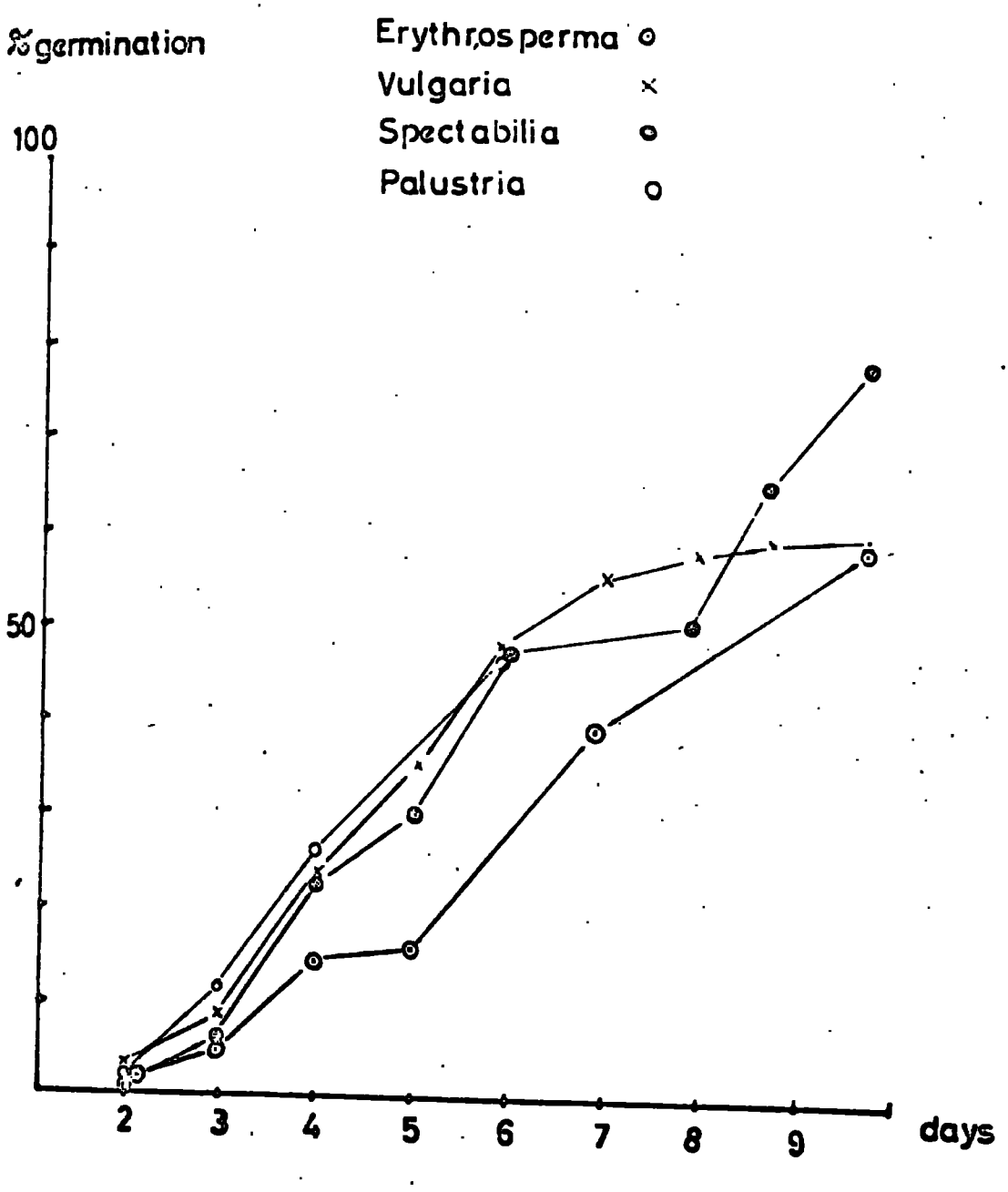
optimal flower-initial formation in Taraxacum which is largely a spring-flowering genus. Buds can be formed during longer light regimes however. Bud formation in June, when the plants are subject to high intensity illumination from outside for 16-18 hours of the day, is still considerable, though lower than in the winter.

Due to these special conditions of growth, which were introduced to give near standard and optimal heat and light regimes, for both rapid generation time and a minimum of environmental variation, watering had to be performed every day. If this was neglected, mildew and the abortion of most buds were rapid consequences.

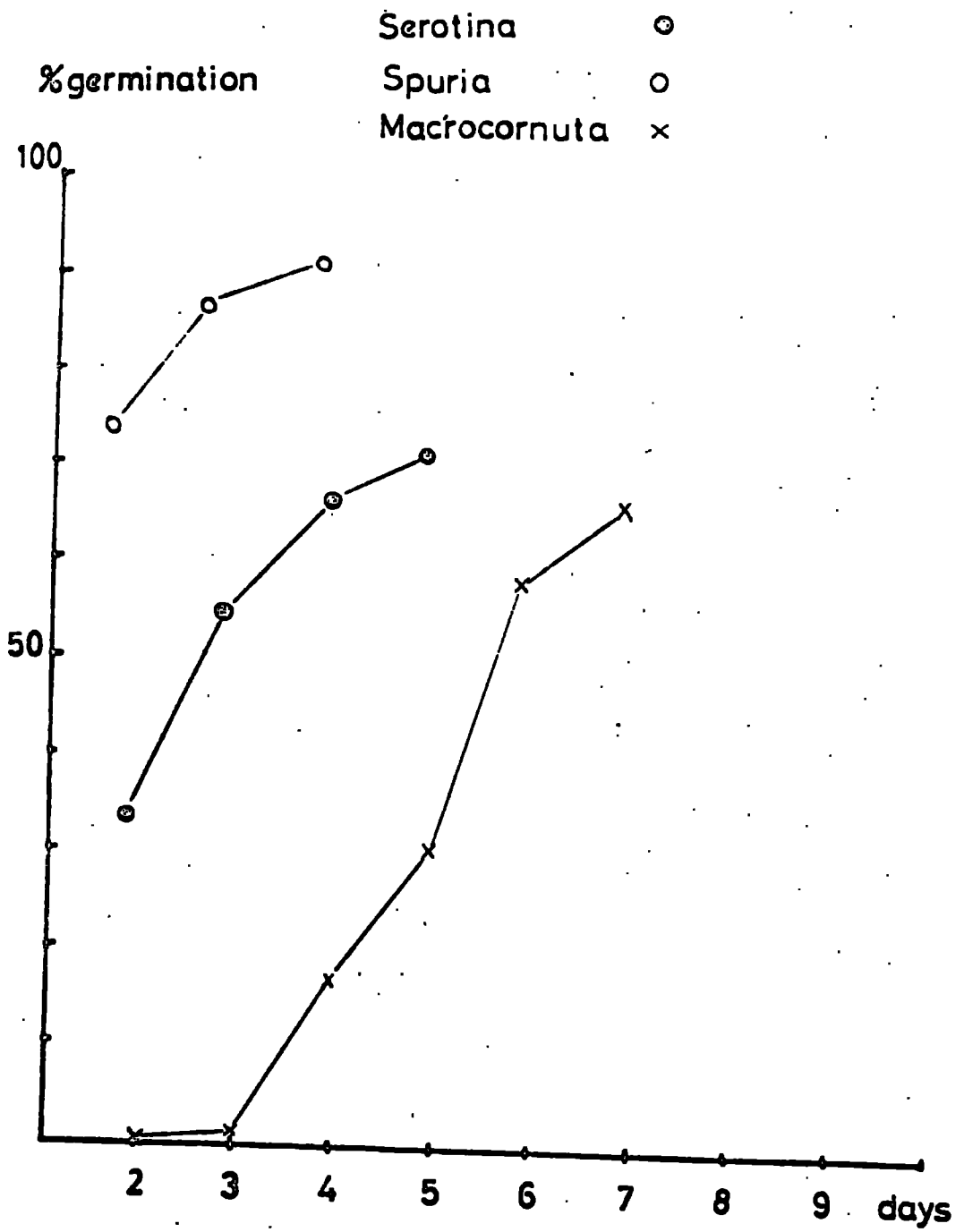
Seed germination rates

Records were kept of the percentage germination of each sample each day. These have been averaged, and appear in graphs 1-3. Of the 4 British Sections, the Vulgaria, Spectabilia and Palustria demonstrate virtually identical germination curves, while the Erythrosperma show a slower germination rate (graph 1).

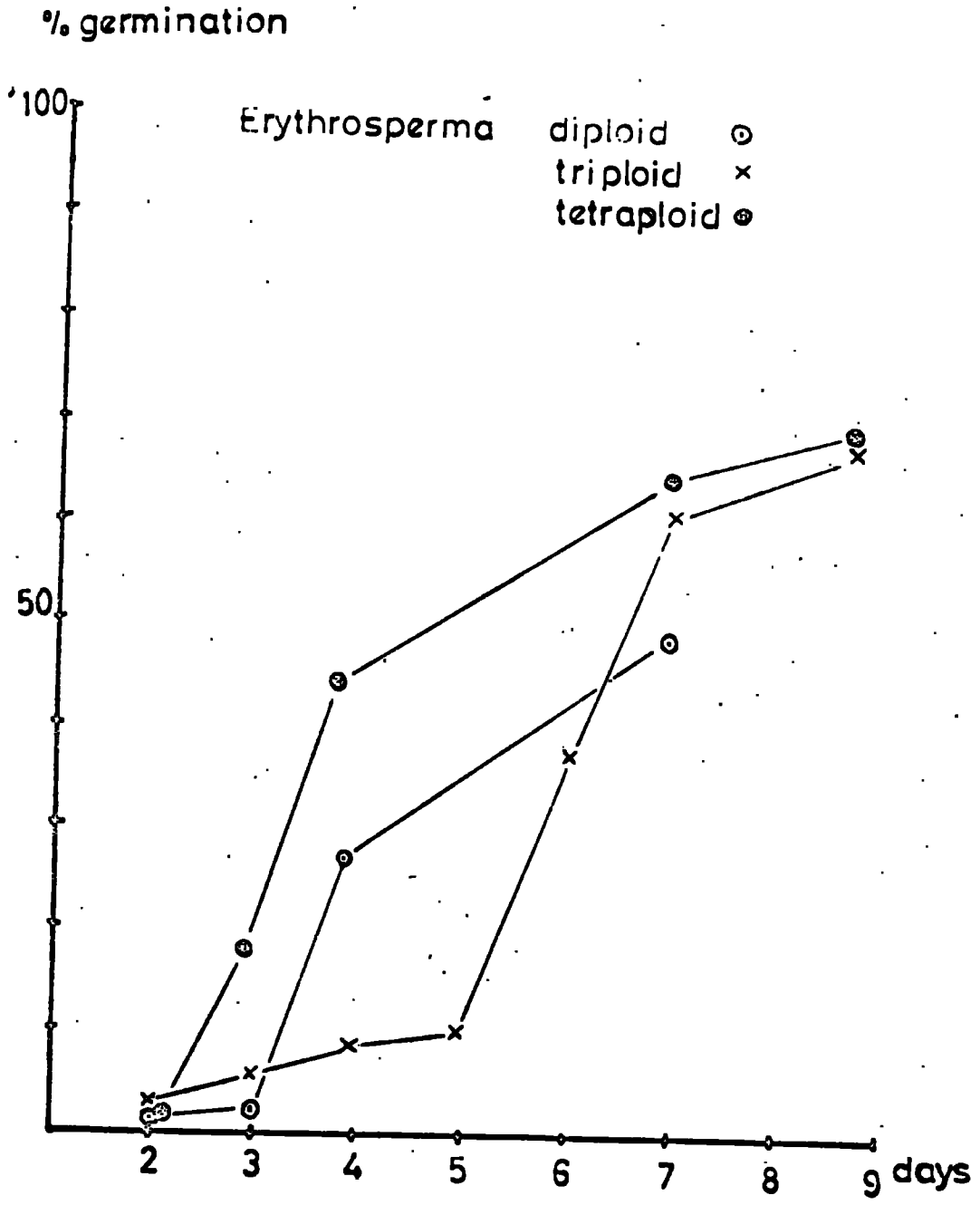
Graph 2 shows germination curves for the other three sections, of which a sufficiently large number of samples have been germinated. The slowest germination rate is shown by the Macrocornuta, of which diploid, triploid and tetraploid species are included. These different chromosome levels all exhibit very similar germination curves, as indeed did all species within any of the sections. A high germination rate is however seen in the diploid Serotina (two species), while the pentaploid Spuria show an extremely rapid germination, far faster than any other found in the genus. This very fast



Graph 1. Germination rates of the Erythrosperma, Vulgaria, Spectabilia and Palustria.



Graph 2. Germination rates of the Serotina, Spuria and Macrocornuta.



Graph 3. Germination rates of diploid, triploid and tetraploid Erythrosperma.

germination, with almost total germination by the third day, is not mirrored by the other pentaploids grown (sub-section Eu-Spectabilia), and no doubt demonstrates the evolutionary isolation of the section Spuria which appears far removed from any other in the genus.

As a contrast, graph three records the germination curves of three closely related species in the Erythrosperma with different chromosome numbers. There is some indication that the triploid may be slower than either the diploid or the tetraploid, an interesting parallel with graph 2, but it is not possible to readily connect chromosome number with the rate of germination.

Growth rates

Eight seedlings were kept from each of the first 100 samples. These were grown in pairs in 4 different soil regimes. These were John Innes No. 3, 1 to 1 John Innes and silver sand, and these two soil types, but with the pots submerged in water to 1 inch from the rim to keep the soil permanently saturated. The maximum leaf-length and width were measured on all plants after 3 months and 6 months. When the plants flowered, a number of quantitative and qualitative characters were noted for each individual. It was hoped to obtain an idea of the inherent plasticity of the British sections by this method.

Four seedlings were kept from each of the second 100 samples. These were all grown in John Innes No. 3 compost, and the same data collected as for the first 100. This was as a control, to determine how much variation, genetic or environmental resulted in conditions as standard as those provided. The remaining 200 samples were grown in duplicate only,

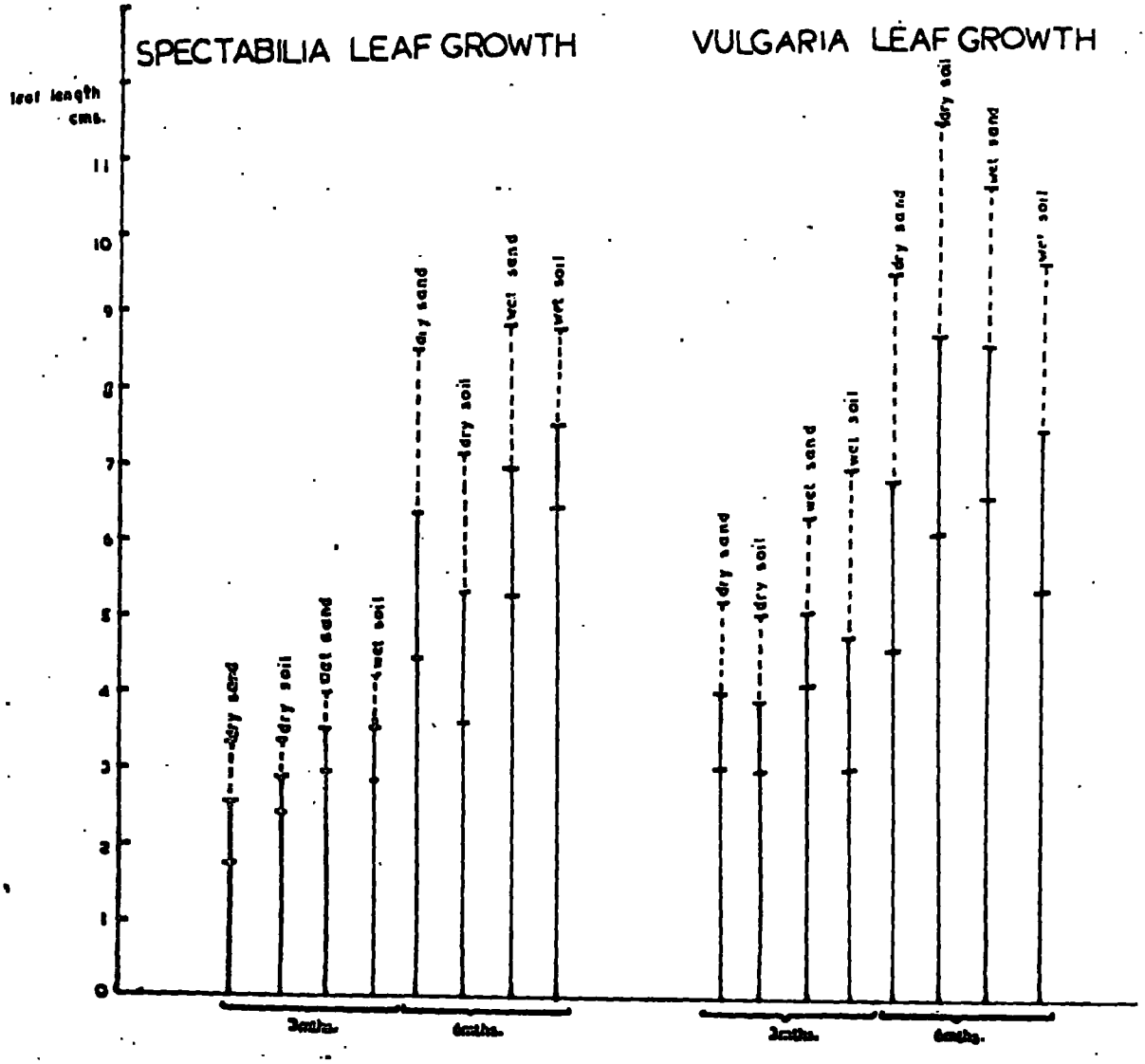
and characters were only taken at flowering for taxonomic purposes.

Graph 4 is a representation using histograms of the mean leaf length and standard deviation of the sections Spectabilia (all T. faeroense) and Vulgaria (various species) at 3 months and six months under the four soil regimes. The standard deviations are large in every case, and very few conclusions can be drawn. The most obvious conclusion is that the standard deviations are larger in the Vulgaria, a conclusion borne out by the examination of other characters and by Griffiths (1924) and Kappert (1954). The Vulgaria also apparently grow faster, and there is some indication that both sections are more successful in the wet regimes. The general conclusion to be offered is that the technique employed is not satisfactory, as any environmental influence is masked by the inherent variability and, or plasticity of the material.

Mean variance

An attempt was made to investigate the variability found within a sample, in other words from a single seed-head, which if apomictic would in theory be genetically uniform, in order to discover how variable plants growing in standard conditions really are. This variability may be genetic, but in all probability is environmental, except in sexual plants, or individuals with a sexual history. Such variation is clearly important to the understanding of the microspecies concept in the various sections. It can be conveniently studied by the examination of the variance shown in samples all grown under standard conditions as the second 100 samples were.

I devised a formula to find the mean variance shown in a number of



Graph 4. Leaf growth at 3 and 6 months in the Vulgaria and Spectabilia in 4 edaphic regimes, with standard variation shown.

characters by a sample. This is

$$\frac{E\left(\frac{E(x-x')^2}{n-1}\right)\frac{100}{x'}}{S}$$

where x is the reading

x' is an artificial mean

n is the number of plants

S is the number of characters sampled

E is 'the sum of'

This formula in fact represents a mean of several readings of variance, standardised to account for the different scales of variability in which the various characters are found. The characters used were the most variable, and those in which three significant figures were usually obtained; namely leaf length, leaf width and capitulum diameter. It is only valid for readings with the same number of significant figures, and is not, I believe an accurate estimation, but merely a rough guide. The combination of a number of characters in a reading of variance is quite invaluable however, and I believe I am right in saying that no such method is in existence, probably because it is difficult to envisage anyone but a taxonomist requiring a similar treatment of data.

With the use of this formula, a Mean Variance can be obtained for a sample which is a measure of the variability shown by this sample in these conditions. A standard deviation can then be readily ascertained to show the statistical separation of the various Mean Variance figures,

and some idea of the variability of samples of different chromosome number, or of different sections can be obtained.

These are shown on Table 3.

Table 3. The Mean Variance of Various Sample-Types

Definition of samples	Number of samples (each containing 4 plants)	Mean Variance	Standard Deviation
Vulgaria (all chromosome numbers)	9	119.2	62.5
Erythrosperma (")	19	119.1	47.6
Spectabilia (")	7	33.5	29.8
Erythrosperma (diploid sexual)	6	171.3	33.0
Erythrosperma (triploid apomict)	10	84.3	27.3
Erythrosperma (tetraploid apomict)	2	139.2	8.7
Spectabilia (triploid)	1	96.3	-
Spectabilia (tetraploid)	5	26.5	15.8
Spectabilia (pentaploid)	1	5.7	-
Vulgaria (triploid)	7	114.7	36.1
Vulgaria (triploid aneuploid)	5	122.8	56.5
Vulgaria (diploid)	1	223.9	-

Two conclusions can be made from this treatment of the variability found in sibling cultures in fairly standard conditions. The first is the very much lower variability shown by the Spectabilia. From the one triploid sample, it seems that this low variability may be restricted to the tetraploid and pentaploid species, which constitute the

vast majority in this section. That this is not a factor resulting from the high chromosome number alone is indicated by the two tetraploid Erythrosperma, which show a high Mean Variance. The triploid Spectabilia (T. naevosum) is very close to the Vulgaria, and on this evidence and the chromosome number, perhaps deserves to be placed in this section. It seems that the Spectabilia may well possess either a lower environmental response, or a higher genetic stability than the other sections, perhaps as a function of their specialised habitat requirements often base rich flushes, at a high altitude. The other two sections are fundamentally plants which colonise bare ground. In these environments, the possession of high plastic or genetic variability might be at a premium.

Plastic response in the field

That the variability shown in greenhouse culture may be at least partly a plastic response to slight environmental variation can be inferred through an examination of plants growing in the field from which a greenhouse culture has been taken. The results here are sometimes startling. T.oxoniense is the commonest species of the Erythrosperma to be found on the Magnesian Limestone grassland in County Durham. The mean leaf length at Sherburn Hill is 51.1 mm., while that of plants grown from seed collected at the same locality is 181.8 mm. (see Table 4). An equally remarkable plastic response to greenhouse conditions is demonstrated in T.hamatum in the Vulgaria. Plants growing with T.oxoniense on Sherburn Hill have a mean leaf length of 37.6 mm., less than that of the latter species, while seeds from the same material grown experimentally

become large plants with a mean leaf length of 237.0 mm. This response to environmental conditions, perhaps largely soil-depth in these instances, is usually most marked in the Erythrosperma, as these are typically plants of xerophyte localities, with shallow soil. In some cases, the Erythrosperma do seem to have a limited capacity for growth however, as is seen in T.rubicundum from Cassop Vale, and to a lesser extent in the Czechoslovakian T. austriacum.

The range of variation in size in a species in one locality can also be striking. Two individuals of T.subcyanolepis in the Vulgaria measured 34 and 194 mm. in leaf-length. These both came from grassland on Sherburn Hill, but whereas the small individual came from short grassland dominated by Festuca ovina and Poterium sanguisorba, the large one came from the Dactylis on the summit, growing in much deeper

In contrast, the Spectabilia show very little response to greenhouse conditions, and the chief variation in leaf-size is that due to the age of the plant. In the sub-sections Crocea and Naevosa, the first year leaves are habitually at least twice the size of subsequent leaves, and are usually of a different shape. This difference can be shown to be absolutely constant in the greenhouse and in the field. The sub-section Eu-Spectabilia do not demonstrate this age-change, and neither in my experience do the Vulgaria, although it has sometimes been reported, and presumably occurs in some species.

Table 4. Plastic response to Greenhouse conditions

Sample	Sample size	Mean leaf-length (mm)
T.oxoniense (Erythrosperma) Short turf, Sherburn Hill Co. Durham.	23	51.1
T.oxoniense (greenhouse)	6	181.6
T.rubicundum (Erythrosperma) Short turf, Cassop Vale, Co. Durham.	7	22.0
T.rubicundum (greenhouse)	10	65.6
T.austriacum (Erythrosperma) Kovacovska, C.S.S.R.	6	73.0
T. austriacum (greenhouse)	11	143.4
T.hamatum (Vulgaria) Short turf, Sherburn Hill, Co. Durham.	7	37.6
T.hamatum (greenhouse)	6	237.0
T.faeroense (Spectabilia) Various localities.	33	68.2
T.faeroense (greenhouse)	9	70.3
(Sub-section Crocea) T.pycnostictum (Spectabilia) From wet cliff, Caenlochan, Angus. (I st. year, greenhouse)	9	174.4
T.pycnostictum (2nd year greenhouse)	7	73.5

Character Variance

It is a well accepted taxonomic precept that some characters possessed by a plant are more liable to plastic response to the environment than others, and that those characters that are least variable are those which are likely to be of the greatest taxonomic value. It is interesting therefore to extend the consideration of Mean Variance (based on the variance of leaf-length, leaf-width and capitulum diameter), and plastic response (in which leaf-length only was used) to other characters. The variance of different characters in different taxa are tabulated below (Table 5). (Characters used as defined in Chapter 4)

Table 5. Character Variance

Section	Character	No. of samples	Mean of character Variance (less than 50 considered unimportant
Erythrosperma	Leaf length	17	186.2
	Leaf width	21	111.4
	Capitulum diam.	22	45.0
	Achene length	23	26.4
	Achene width	21	128.0
	Cone length	21	273.5
	Rostrum length	21	165.1
	Bract length	24	48.4
	Bract width	24	6.9
	Bract length/width	24	18.5
Vulgaria	Leaf length	9	216.7
	Leaf width	9	94.7
	Capitulum diam.	9	14.7
Spectabilia	Leaf length	7	50.3
	Leaf width	7	42.4
	Capitulum diam.	7	46.6

It will be noticed that in addition to the very variable characters of leaf length and leaf width, achene width (but not length) and the lengths of the cone and the rostrum to the achene are extremely variable even in stable conditions (as here), and may not be very suitable taxonomic characters. Of these characters, the last two only are of taxonomic importance.

Multimedium Cultures

An analysis was also made of the variability of those plants (the first hundred samples) in which siblings were subjected to different soil media. These will be known as multimedium cultures. For these, means were calculated for each of the paired culture-types in a sample, for a number of characters, both qualitative and quantitative (as defined in Chapter 4). When the means of a character differed markedly for different culture types for a number of samples, the means of the sample means for a character were compared for the different culture media. A sigma test of significance was performed for these composite means, to inspect the apparent environmental effect of this character. P=0.05 was used as the level of significant difference. The results of these analyses are presented in Table 6. This treatment of the data is probably less satisfactory than the mean variance technique, because the variance inside a culture type cannot be shown. It should be emphasised that this technique of comparing means by the sigma test cannot be used for measurements of variability in single medium cultures, and it is employed here for purposes of comparison with the mean variance technique. In point of fact,

I find this latter technique much more preferable for the analysis of variability.

It would be expected that where a number of different culture media have been used, that the resultant variability of the plants would be greater as a result of environmental response by the individual plants. Several of the characters which showed an unimportant mean variance in the single culture tests (less than a value of 50), showed much larger variability under a multimedium regime. We thus have considerable evidence that much of the variability in Taraxacum may be plastic response to the environment, although it is still not clear whether the variation in single culture samples is also of this nature.

Table 6

Character	Section	Medium	Mean	Sample	P
Presence of brown in achene	Vulgaria	Dry sand	73.1%	19	
		Dry soil	75.8%	22	
	Spectabilia	All	0%	5	
Presence of violet or purple in ligule	Vulgaria	Dry sand	33.3%	18	
		Dry soil	47.4%	19	
Presence of red or purple in exterior bract	Vulgaria	Dry sand	25.0%	20	
		Dry soil	13.1%	23	
Presence of red or purple on scape	Vulgaria	Dry sand	42.8%	21	
		Dry soil	44.4%	27	
Presence of red or purple on petiole	Vulgaria	Dry sand	88.0%	25	
		Dry soil	84.8%	33	
Presence of hairs on scape	Vulgaria	Dry sand	45.6%	22	
		Dry soil	28.6%	28	
Presence of colouring on leaf	Vulgaria	Dry sand	33.3%	24	
		Dry soil	15.6%	32	
Exterior bracts glaucous	Vulgaria	Dry sand	52.5%	19	
		Dry soil	78.5%	23	
Exterior bract length	Vulgaria	Dry sand	7.72mm	19	.04
		Dry soil	8.87mm	20	
Exterior bract width	Vulgaria	Dry sand	2.027mm	19	.06
		Dry soil	2.348mm	20	

Table 6 cont.

Character	Section	Medium	Mean	Sample	P
Exterior bract length/width	Vulgaria	Dry sand	3.93	19	
		Dry soil	4.14	20	
Achene length	Vulgaria	Dry sand	3.01mm	27	
		Dry soil	3.16mm	29	
		Wet sand	3.00mm	5	
		Wet soil	2.92mm	6	
	Spectabilia	All	2.88m	5	
Achene cone length	Vulgaria	Dry sand	.345mm	24	.10
		Dry soil	.414mm	27	
	Spectabilia	All	.420mm	5	
Rostrum length	Vulgaria	Dry sand	7.80mm	27	Dry sand/ Dry soil 0.001
		Dry soil	8.98mm	27	
		Wet sand	8.80mm	5	
		Wet soil	8.91mm	6	
	Spectabilia	All	7.16mm	5	
Spinulation of Achene Scale 0-5	Vulgaria	Dry sand	2.37	27	
		Dry soil	2.72	29	
		Wet sand	2.40	5	
		Wet soil	2.83	6	

Table 6 cont.

Character	Section	Medium	Mean	Sample	P
Leaf length	Vulgaria	Dry sand	67.9mm	74	Sand/soil .0009
		Dry soil	82.2mm	58	Sand/Wet sand .01
		Wet sand	61.6mm	17	Soil/Wet soil .06
		Wet soil	72.6mm	12	Wet sand/Wet soil .023
	Spectabilia	Dry sand	58.5mm	29	Sand/Soil .065
		Dry soil	50.2mm	29	Sand/Wet sand .002
		Wet sand	72.4mm	29	Soil/Wet soil .0001
		Wet soil	74.6mm	27	Wet soil/ Wet sand .72
	Erythro-sperma	Dry sand	52.4mm	11	Sand/Soil .80
		Dry soil	54.4mm	11	
Leaf width	Vulgaria	Dry sand	21.4mm	74	Sand/soil .0008
		Dry soil	26.1mm	58	Sand/Wet sand .01
		Wet sand	17.5mm	17	Soil/Wet soil .015
		Wet soil	22.7mm	12	Wet sand/ wet soil .003
	Spectabilia	Dry sand	11.9mm	29	Sand/Soil .085
		Dry soil	10.0mm	29	Sand/Wet sand .15
		Wet sand	10.3mm	29	Soil/Wet soil .003
		Wet soil	12.5mm	27	Wet sand/ wet soil .01
	Erythro-sperma	Dry sand	15.18mm	11	Sand/Soil
		Dry soil	15.27mm	11	

Table 6 cont.

Character	Section	Medium	Mean	Sample	P
Calathium diameter	Vulgaria	Dry sand	33.6mm	16	Sand/Soil .7
		Dry soil	36.7mm	18	
Ligule width	Vulgaria	Dry sand	2.29mm	16	Sand/Soil
		Dry soil	2.20mm	18	

In conclusion, the following characters have not been shown to be liable to excessive environmental variation.

Diameter of capitulum.

Width of ligule.

Stripe on ligule red or purple.

Width of exterior bract.

Presence of red or purple colouring on bracts.

Presence of glaucous bloom on bracts.

Presence of red or purple colouring on scape.

Presence of indumentum on scape.

Presence of red or purple colouring in petiole.

Presence of coloured blotches on leaf.

Length of achene.

Spinulation on achene.

Presence of dark brown pigment in achene.

In comparison, the following characters displayed some considerable plastic response to the environment (or genetic heterogeneity?) and are of doubtful taxonomic use (those marked with an asterisk are used in the section in which plasticity has been shown).

* Leaf length. (Not Spectabilia)

* Leaf width. (Not Spectabilia)

* Exterior bract length (?Not Erythrosperma)

Achene width.

* Length of cone to achene.

Length of rostrum to achene.

Chapter 4

NUMERICAL TAXONOMY

Numerical taxonomy is a relatively new, exciting technique, which has caused a great deal of discussion and controversy. This may be because it has been used, mostly in lower plants, as a definitive technique - one that will handle a taxonomy without further subjective manipulation by the taxonomist. This may be satisfactory, or even necessary in the Bacteria and the Fungi. In higher plants, where so much more may be known about breeding barriers, gross morphology and cytology, it is a less satisfactory technique, and is best used as an additional guide to relationships.

In numerical taxonomy, the processes are purely mechanical and require no more than a certain arithmetical dexterity, and a great deal of patience, unless one has access to a computer. The skill, which will determine the success or failure of the operation and the usefulness of the resulting taxnomy, lies in the choice of characters and the choice of samples, not in the choice of species. The samples that are chosen are known in the jargon as Operational Taxonomic Units, or O.T,U.s, and as such they will be hereafter referred. These are the representatives of the taxa one wishes to classify.

Technique

A very careful examination of all possible characters in the genus was made. Characters which can be used for a simple numerical taxonomy

have to obey the following requirements:

1. Characters should be readily divided into 'present or absent' categories.
2. In any group of O.T.U.s, present or absent should not exceed 90%.
3. The character should not be linked with any other character used, but should vary independently.
4. The character should not be liable to excessive environmental plasticity.
5. The character used should not be part of another character used, (e.g. one cannot use 'rostrum nil, rostrum present' in the same treatment as 'rostrum more than 7mm., less than 7mm').
6. The character should be determinable on living material, dried material, and from good type descriptions.

50 characters were chosen that obeyed these conditions. 50 were chosen in order that a percentage determination of the coefficient of similarity might be readily be made without a greater arithmetical effort than it requires to multiply by two. The characters that were used are set out in table 7. For each sample that was to be used as an O.T.U., a punch card was punched for the presence or absence of the 50 characters on a predetermined basis. An example of the type of punch-card used is shown in fig.

The project was severely handicapped by the low number of O.T.U.s used. This limitation was necessitated by a number of factors. The need to use type descriptions of the taxa, rather than relying upon my own descriptions of material growing in standardised conditions was due

to difficulty in obtaining a sufficiently large number of species in cultivation. Many type descriptions are unsatisfactory however, either in their general lack of information (most of the Handel-Mazzetti types fall into this category) or because the characters of the achene were not available to the author. Obtaining the types of many hundred species seemed an impossible task to accomplish in the time, so it was decided to use type descriptions, but to exclude those that were unsatisfactory. At the time of this work, I was unable to obtain, or in some cases unaware of the existence of several important papers on the taxonomy of Taraxacum. Indeed, several of van Soest's most important and informative papers have appeared since I finished the numerical taxonomy section of my work.

In addition to the punch cards made out for type description punch cards were also made for all samples grown from seed (and the few propagated from roots collected from roots in the wild) in the greenhouse. It is hoped at some future date that the cards from a rather large number of species grown in a standard environment (at the moment about 120 species in 23 sections have been cultivated) can be compared with punch cards made out for all the types, using the description and the type specimen. As this treatment will entail the ordination of well over 2000 O.T.U.s, and will thus involve the calculation of a minimum of 2,000,000 coefficients of similarity, it will be done with the aid of a digital computer, for which a number of excellent numerical taxonomy programmes exist.

In order to carry out a numerical taxonomy, a number of cards representing O.T.U.s from type descriptions was assembled. These would belong to a section, or a number of smaller related sections. By comparing

Table 7. Association Characters for Numerical Taxonomy

	Punch		Leave
1	Achene length	>3.5 mm	3.6? mm
2	Achene width	>0.9 mm	1.0? mm
3	Achene l/w	>3.5 mm	3.6? mm
4	Cone length	>0.6 mm	0.7? mm
5	Achene	smooth	rugose
6	Spines on achene	short (0.1 mm)	long (0.2 mm)
7	Extent of spinulation	0-2/s	3-5/s
8	Achene pigments present	sand	or not
9	"	brown	"
10	"	grey	"
11	"	red	"
12	"	violet	"
13	"	cinnamon	"
14	Achene	dark	"
15	Rostrum length	> 7.0 mm	7.1> mm
16	Achene	tapered	or not
17	Plant	sexual	or apomictic
18	Pollen present		or not
19	Exterior bracts dentate or ciliate		or glabrous
20	Exterior bracts of a different colour on each side		"
21	Exterior bracts adpressed to erect		or reflexed
22	Exterior bracts ovate to ovate-lanceolate		or linear-lanceolate
23	Exterior bracts marginate		or not (see photograph 3)
24	Exterior bract coloured		"
25	Exterior bracts glaucous		"

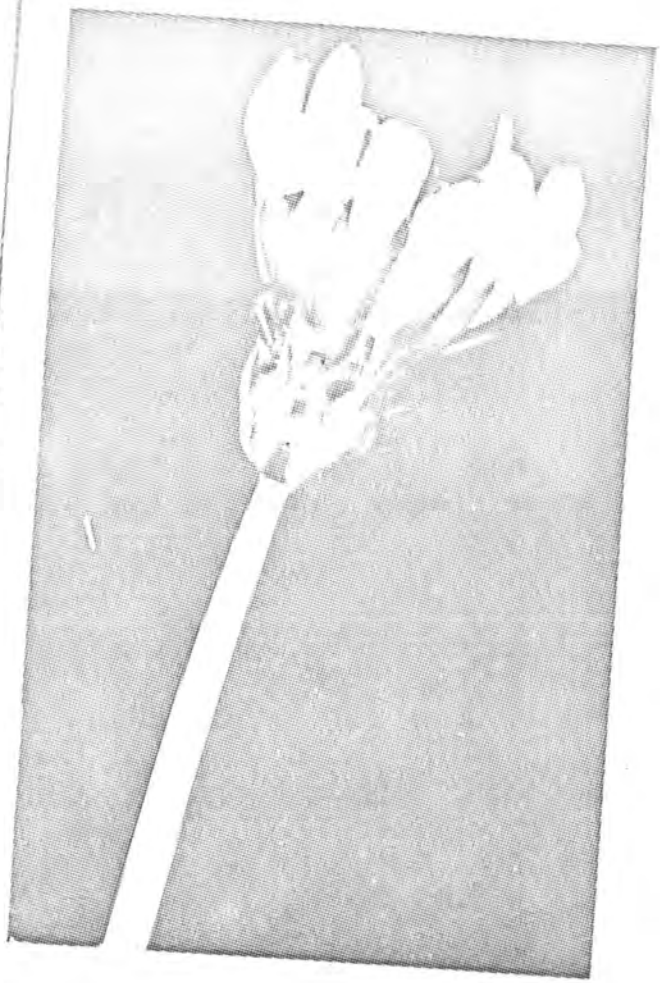
Table 7 cont.

	Punch	Leave
26	Exterior bracts dark	or not
27	Interior bracts dark	"
28	Interior bracts glaucous	"
29	Interior bracts corniculate	" (see photograph 2)
30	Ligules purple to red, including violet	"
31	Ligules involute	"
32	Calathium >35 diam.	Calathium 36> mm diam.
33	Style and stigma yellow	or not
34	Scape coloured	"
35	Scape glabrous	"
36	Scape less than ½ leaf length	"
37	Petiole more than a ¼ leaf-length	"
38	Petiole winged	"
39	Petiole coloured	"
A	Leaf glabrous	"
B	Leaf glaucous	"
C	Leaf dark	"
D	Leaf incised to ⅓ distance to mid-rib	"
E	Leaf acuminate dentate	or acute dentate
F	Terminal lobe acute	or rounded
G	Leaf >169 mm long	leaf 170> mm long
H	Leaf > 44 mm broad	leaf 45 > mm broad
I	Leaf l/w > 4.4	leaf l/w 4.5>
J	Leaf lobes l/w > 3.9	leaf lobes l/w 4.0>
K	Leaf lobes recurved	patent or squarrose

Selection Characters.		Punch.	
XZ	Vulgaria	A	Aneuploid
Y	Erythrosperma	E	2n = 16
W	Spectabilia	1	2n = 24
UV	Palustria	0	2n = 32
T	Fontana	U	2n = 40
S	Alpina		
R	Ceratophona	L	Dyads 25% +
Q	Serotina	M	Triads 25% +
P	Macrocarnuta	N	Tetrads 60% +
O	Others		

Note: "Punch" means cards for O.T.Us passessing the character-state should be punched at the relevant hole.
"leave" means cards for O.T.Us passessing this character-state should not be punched at the relevant hole.

The selection characters on this page are for sorting purposes only and are not used in the numerical taxonomy.



Photograph 3 Taraxacum stevenii head, demonstrating the very wide scarious margins to the exterior bracts, as is found in the Palustria, Scariosa and several primitive sections.

x 2

the punched edges of two cards, it is possible to determine the number of presence and absence characters two O.T.U.s shared in common. This figure was multiplied by two to give a percentage reading of similarity between the two samples. This is the coefficient of similarity, which is calculated by $(\frac{x}{a+b})$ 100 where x is the number of characters the samples have in common, and a and b are the number of characters in each sample (in this case 50).

The coefficients are calculated between all the O.T.U.s involved in an operation. A type of shading is decided to denote different classes of similarity. I used black to denote 85% and above, checks, 75% and above, and squares, 65% and above. No shading denotes a coefficient of similarity between two O.T.U.s of under 65%. The O.T.U.s are then shuffled along the axis of a Kulczinsky square until the most satisfactory ordination is achieved. This will be when the most closely similar taxa are adjacent; but in the large ordinations of entirely apomictic aggregates such as the Palustria, Spectabilia and Erythrosperma, where relationships are very complicated and 3-dimensional, it may be when the O.T.U.s of high similarity are central, and those of low similarity are marginal.

Now one may see where the groupings lie. It is possible to programme computer techniques so that the computer decides on the groupings at a certain order of similarity which the taxonomist decides. In my case, with manual operation, the grouping was more subjective than this. An indication of some suggested groupings are presented with the Kulczinsky squares representing ordinations, shown in diagrams 1-7.

Diagrams 1-7. Numerical taxonomic ordinations. See chapter 4 for further information.

Section SPECTABILIA Dahlst

Section PALUSTRIA Dahlst

GHYZ
CANADENSE
CORNUTUM
section CERATOPHORA Dahlst
kok-saghyz
lehrianum
saltcanum
pseudo norvegicum
russeolum
norvegicum
tornense
cornutum
hjeltii
perlatescens
hultenii
simulum
lactucaceum
krattlii
platyceras
gallicum
saltcanum
pseudonorvegicum
russeolum
norvegicum
tornense
cornutum
hjeltii
perlatescens
hultenii
simulum
lactucaceum
krattlii
platyceras
gallicum

sections CUCULLATA V.S.

FONTANA V.S.

sections ARCTICA Dahlst
GLABRA Dahlst PACHERA V.S.
PARVULA H.M. RHODOCARPA V.S.

section ALPINA Haglund

OREOPHILUM ALPINUM

oreophilum
apenninum
pseudalpinum
helveticum
corinthiaceum
parssenense
pseudofontanum
vernejense
vereinse

...ilum
...inum
...pinum
...icum
...ceum
...ense
...anum
...lense
...nse

Sections GLACIALIA HM OBOVATA V.S.

SEROTINA V.S. LEPTOCEPHALA V.S. SCARIOSA Dahlst

My chief consideration in embarking in a programme of numerical taxonomy in Taraxacum was to see if species could be grouped into a unit inside a section which was workable. The advent of 'Flora Europaea' required that a treatment valid throughout Europe be devised which did not encompass all the European species, which at over a thousand in number are somewhat unwieldy. Furthermore, a great deal of work was necessary before it could be finally decided which of the microspecies could be regarded as reliable. There seemed four other possibilities apart from using the microspecies.

The first, the maintenance of Handel-Mazzetti's account in his 'Monographie der Gattung Taraxacum', 1907, written before the microspecies classification got under way in the genus, seemed untenable as even major groupings in the genus have altered since his day, and many of his species have very heterogeneous types (T.indicum for instance has a type containing no less than 4 present-day species).

The second possibility was the maintenance of the present-day sections, either as sections, or as aggregate or 'sensu lato' species. This idea has much to commend it, but the variation in the genus seems to be inadequately represented, even for a condensed Flora such as this.

A third possibility was that more aggregate species be created on the basis of subjective, or 'classical' taxonomy. In other words, where it was felt that a section could be usefully subdivided into further aggregate species, these species should be described as new 'sensu-lato' species. It was felt that the execution of this exercise might be aided by the numerical taxonomy of some of the more critical groups, the fourth

technique considered.

Due to the drawbacks mentioned in the part of this chapter concerned with technique, the most difficult section of all, the Vulgaria has not been tackled at all. Nevertheless, the treatment of the Palustria is as complete as type descriptions allow, and those of the Alpina, Fontana, Coratophora, Spectabilia and the primitive sections are probably complete enough to give a representative picture of grouping in these sections. A treatment of the Erythrosperma, Eu-Erythrocarpa and Obliqua is the largest treatment attempted 70 O.T.U.s being ordinated together. Unfortunately this did not account for the species in these groups recently described, nor did I have the information now available to me on the more obscure species which is given in The Catalogue of the Erythrosperma (van Soest 1966c). Both in the treatment of this group, and the Spectabilia there are sharp disagreements between some of the groupings arising from the numerical taxonomy, and van Soest's judgement of where probable relationships lie. In many cases there were also agreements, and the technique did not appear to be totally without merit, many of its undoubted shortcomings being due to the poor quality of some of the information fed into the system. A vivid example of how misleading the results could be was in the Rhodocarpa. I used two taxa, T.rhodocarpum and T.schroeterianum as two O.T.U.s, unaware that they were in fact synonyms (at that time there existed nothing in the literature to tell me otherwise), and the two O.T.U.s, although adjacent showed a low level of relationship! This was , no doubt, due to the very different quality of the type descriptions of T. rhodocarpum (Dahlstedt) which like the rest of his work at this time

was a model of perfection and of T.schroeterianum (Handel-Mazzetti) which, also true to type, was an atrocity! Luckily this was the sole Handel-Mazzetti description that I was forced to use, and the majority of types in the genus are very good. Nevertheless, I remark upon this example in order to emphasise the unreliable quality of this work. I would not wish it to be thought of as definitive, although I think it has some value.

I have discussed these treatments very fully with van Soest, and I am in continuing correspondence with him about the 'Flora Europaea' account. I have believed from the beginning that the results of the numerical taxonomy must not be used in any way, unless supported by strong experimental and morphological data. In many cases groupings arising from the numerical taxonomy have been disregarded as of little value (e.g. the separation of T.graiense from the main body of the Fontana, or the similar separation of T.oreophilum from the Alpina), or even pure nonsense (as in the grouping of T.litanderi in the Pachera (now included in the Laevia)and T.rufocarpum in the Laevia sensu Schischkin). In other cases van Soest and I had a strong feeling that the results of the numerical taxonomy were supported by other data. For instance the idea that the Palustria was a homogenous group that could not be usefully separated is borne out by the numerical taxonomy of this group (diagram 2). In the Ceratophora, a clear demarcation appears between the European and some of the Canadian taxa, a grouping which had previously been suspected, while the Erythrosperma show an interesting justification for the use of achene colour as an important taxonomic character. The grey-brown species, T.simile, T.dissimile and T.isthmicola show a close relationship with the

Obliqua, which have the same coloured achenes. Similarly, the large fulvous achened species T.fulvum, T.falcatum and T.fulvicarpum (the last often treated as Spectabilia) are grouped, as are the southern European fulvous achened species T.squamulosum, T.spinulosum, T.stenospermum, T.oxoniense and T.fulviforme. The interrelationships in the Erythrosperma are too complicated to be shown on a 2-dimensional diagram however, and indeed all the 'advanced' sections that have been treated show a very complicated relationship in depth. Note, for instance in the Spectabilia how the central members of the T.spectabile agg. show a relationship with such Naevosa as T.maculigerum and T.firmum, as well as with the plants near T.praestans, which are relatively unrelated to the T.maculigerum group.

Indeed, it became increasingly evident as work progressed that whereas in the more primitive, largely sexual sections relationships were clear-cut and 2-dimensional (witness the ordination of the Glacialia, Serotina, Obovata, Lepto cephala and Scariosa), in the more advanced sections they were not. This is doubtless due in part to the greater differentiation of the sexual species. Nevertheless, an interesting feature of the ordination of the advanced sections was that some species have a high overall similarity with other species, while other species have a very low overall similarity. I suggest that the species of high similarity may have arisen from the main line of descent of the section, perhaps after apomixis had arisen in these plants. The species of low similarity on the other hand may have branched off the main stock early, perhaps while apomixis was not yet widespread, and while they were still

sexual, evolved rather rapidly to their present isolated position in the section. Such a rapid change in the genetic structure of an individual population might be effected particularily in populations of sexual plants occurring in areas where apomicts had become more frequent. In such a situation, at least partial genetic isolation from the apomicts might be achieved, particularly if the apomicts produced no pollen, or diad pollen, as it is likely that the early apomicts would (see diagram 11). In this kind of population structure, the sexual gene-pool might become very limited, and random fluctuations of gene-proportions (gene- drift) would be prominent. In this way non-adaptive or only slightly adaptive speciation would readily occur.

In many cases, the groupings have been ignored for the purposes of Flora Europaea, and only when it is felt that the groupings are well warranted have they been used. Both for Flora Europaea and for the general purpose of referring to the groupings arrived at by numerical taxonomy, a system had to be devised for naming the aggregates. This follows the Rules of Botanical Nomenclature as far as possible but introduces some new concepts, the situation not having arisen before, as far as it is known.

If a name exists which agrees, without ambiguity with the new aggregate, this name has priority, and should be used with the authority, followed by 's.l.'. (In fact this taxon would not be of a sensu lato status, having already been described to encompass the broad definition as I wish to use it. Nevertheless, it is agreed between Dr. Walters (family editor) and Mr. Sell of Cambridge, Professor Valentine and myself that all

aggregate taxa in Flora Europaea as found in apomictic groups should be designated 's.l.' to avoid confusion with the microspecies.) Example: T.vulgare (Lam.) Schrk s.l.; for the section Vulgaria, maintained as a single, large, very variable and thoroughly indivisible (except as microspecies) taxon for Flora Europaea.

If a name does not exist which precisely defines the aggregate, the oldest valid name in the microspecies inside the aggregate should be employed, followed by the authority, and s.l.. Example: T.unguilobum Dt.s.l., a small but distinct aggregate taxon which both numerical and conventional taxonomies agree should be described in the Flora.

If a species is maintained by itself, the correct name is presented, but without s.l.. Example: T.glaciale H.M..

Chapter 5

EMBRYOLOGY

As the embryology of Taraxacum is already well documented, it would be superfluous to present more than a rough sketch of the processes here, with some comment on my own work in this field. For a fuller account, the investigator is recommended to the papers of Gustafsson (1933, 1934a,b), Małecka (1961), Haran (1952), Sears (1917), and Poddubnaja-Arnoldi and Dianova (1934), Poddubnaja-Arnoldi (1939a, b). From these and other works, the following picture of the embryology of Taraxacum has emerged.

The female meiosis in apomictic Taraxaca is, according to Gustafsson (1934b), rather complicated. The chromosomes do not pair at pachytene, and develop through to late diakenesis as univalents, kept apart apparently by some 'mutual repulsion'. At metaphase, this mutual repusltion ceases, and the chromosomes come together in 'secondary associations', in much the same frequency as the more straightforward male meiosis. Thus if the male meiosis is 'low association' with mostly univalents, there will be few secondary associations in the female meiosis. Conversely, if the male meiosis is of a 'high association' type, with mostly bivalents, and some trivalents and univalents, the secondary associations of the female meiosis will be of this type. It seems clear that the secondary associations result from the same kind of mutual attraction of homologous chromosomes which causes pairing at pachytene in a conventional meiosis, but that due to a repulsion in the earlier stages,this cannot take expression until metaphase I, and chiasmata are not formed. The chromosomes spread out along the

spindle to the poles, but they do not resolve into telophase nuclei, and a membrane forms around an elongated restitution nucleus. A homotypic meiosis II results in two diploid diad nuclei. The micropylar diad degenerates, and the antipodal diad develops to form an 8 nucleate embryo-sac in the usual manner for this family. Gustafsson (1933) claims to have observed a pseudohomotypic meiosis, in which the chromosomes as univalents at metaphase I divide homotypically to result in two diploid interphase nuclei, which then behave as the diads in the semi-heterotypic method formerly mentioned, resulting in an embryo-sac. Fagerlind (1947) doubts the existence of this method, which, if it exists must be exceedingly difficult to detect in view of the fact that the meiosis is not simultaneous.

The egg-cell and the fused polar nuclei of the embryo-sac develop autonomously into embryo and endosperm respectively about 36 hours before anthesis in the apomictic Taraxaca. The endosperm, which has twice the chromosome complement of the plant, develops slowly, and 24 hours before anthesis it may be still at the 4-cell stage, while the embryo has reached the 16 or 32-cell stage of development. By anthesis, the two tissues reach a roughly equal cell number however. In experimental work the precocious development of the embryo is of some value, as examination of the ovules some 24 hours before anthesis will show whether or not the ovules are behaving apomictically. Unfortunately, the absence of embryo formation does not automatically indicate the presence of sexuality. It has been shown by Haran (1952) that up to 10% of the

Photograph 4. L.S, of ovule of triploid T. isophyllum, 24 hours before anthesis, showing mature, undeveloped embryo-sac with fused polar nuclei (below) and egg-cell. Paraffin section with Feulgen staining.

x 1200

Photograph 5. Ovule of triploid apomictic T.hamatum, 24 hours before anthesis, showing withered embryo-sac (near bottom) Pectinase dissection technique, with Feulgen staining.

x 800

embryos may not develop in a plant which is quite incapable of sexual behaviour due to a very low rate of synapsis at meiosis. It is likely that this incomplete seed-set may be due to a little synapsis in some ovules, with the resultant loss of chromosomes from some restitutional nuclei. In these ovules, the embryo-sac withers if the egg-cell has not developed before anthesis (photograph 5), and it is probably practicable to detect sexuality by the presence of undeveloped, but unwithered embryo-sacs 24 hours before anthesis.

The embryology of the sexual species has been fully described by Poddubnaja-Arnoldi (1939) and Małecka (1961). This differs from that of the apomicts in the meiosis, which is fully synaptic and regular in most instances, and in the fertilisation of the egg-cell and the fused nuclei by the generative nuclei of the pollen tube. The fertilisation of the egg-cell, and of the fused polar nuclei does not differ from that of other sexual members of the Compositae. Małecka (1965) reports some meiotic disturbances in the anthers of Taraxacum serotinum, a wholly diploid sexual species, and this may also occur in T.pieninicum (Małecka 1961). I have found no such disturbances in the meiosis of the diploid plants with which I have worked.

In Chapter 8, I report the finding of triploids which are apparently facultatively apomictic. It seemed very important to examine the embryology of these plants for confirmation of this partial sexuality; and also to discover whether the female meiosis in these plants was synaptic, as I had surmised. The technique used was that of paraffin-wax sectioning, as described in appendix 1.

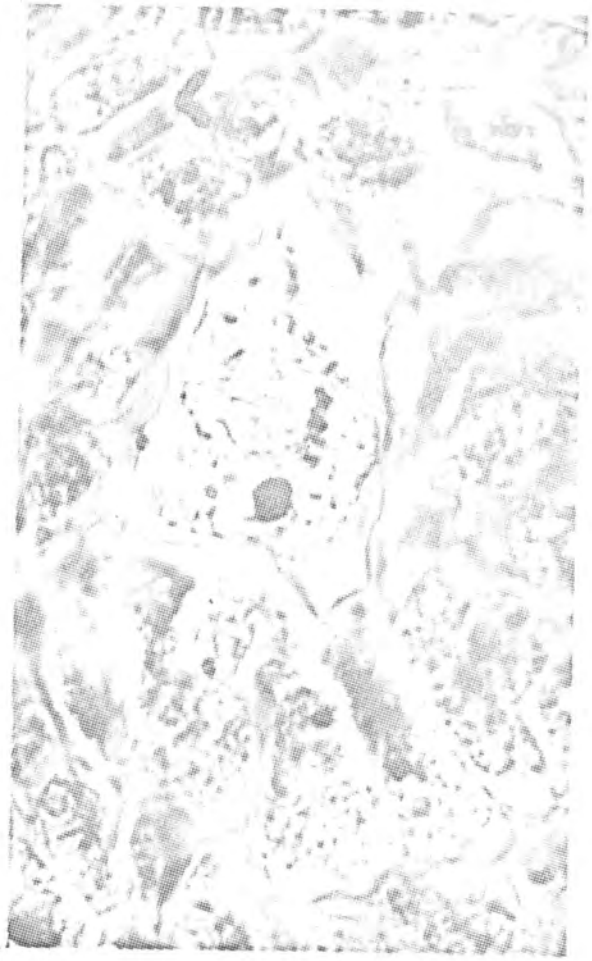
In the triploid plants which were thought to possess some sexuality,

(triploid T.isophyllum from Kovacover Kopce), I examined the ovules 24 hours before anthesis. At this stage nearly all the embryo-sacs of an obligate apomict (as in most tripoids, and all higher polyploids) would have developed into embryos, and the rest withered. As I had expected however, the presumed facultative apomicts from populations containing sexual diploids, showed a high percentage of undeveloped, but not withered embryo-sacs. An example is shown in photograph 4. These had precisely the appearance of sexual embryo-sacs, and it presumed that this is what they were . About 30% were of this type, the rest already being 32 to 128 cell stage embryos. This proportion of sexual embryo-sacs agrees well with the percentage bad seed-set of these plants, and the percentage of sexual diploid off-spring which arose when these plants were pollinated with diploids.

Buds were also examined at an earlier stage (about 4 days before anthesis) in these plants. From these preparations, two stages of female meiosis were obtained (photographs 6 and 7). These are not easy to analyse, but it is clear that the centrometers are pulling apart vigorously in the metaphase, which implies that associations with chiasmata are present. The very exact orientation upon the spindle also suggests that this is a meiosis with primary rather than secondary associations. The second photograph shows the spindle very clearly, and one set of telophase I chromosomes, the other presumably being lost on this section (I was only keeping one section in 3, so this cannot be verified, but the spindle is tangentially orientated to the section.) In this preparation, there is no suggestion of restitution. Although the embryological

Photograph 6. T.S. of ovule of triploid T.isophyllum, showing a synaptic female meiosis, at metaphase I. Paraffin wax section with Feulgen staining.

x 2000



Photograph 7. T.S. of ovule of triploid T.isophyllum, showing a synaptic female meiosis, at anaphase I. Only one pole is in the section, but the spindle is visible. The large black body is an artifact. Paraffin wax section with Feulgen staining.

x 1200

Photograph 8. T.S. of ovule of T. brachyglossum showing the 2-nucleate stage of the young embryo-sac. Note the aborting micropylar nucleus to the left. Paraffin wax section with Feulgen staining.

x 2500

Photograph 9. Embryo-sac of triploid apomictic T.hamatum, showing formation of young embryo (lower right) with undeveloped one-cell endosperm (just to the top left of embryo) 24 hours before anthesis. Pectinase dissection technique with Feulgen staining.

x 800

evidence for facultative apomixis in high association type triploids is not as complete as I would wish, it is, I think now proven for at least some of these plants, and, in addition, a synaptic reductional female meiosis has been shown to occur in polyploids which are in part apomictic. I will use this evidence in chapter 8 to suggest, with the help of other data that the nature of the meiosis is the controlling factor in determining the reproductive behaviour of a Taraxacum ovule.

Chapter 6

CYTOLOGICAL VARIATION

In this chapter I wish to make a brief survey of the occurrence of aneuploidy and cytological chimaeras in Taraxacum. Although these are phenomena which have been but rarely recorded in the genus, I hope to show that both are rather frequently met with in some apomictic sections.

Aneuploidy

No cytological work in the genus previous to Sörensen and Gudjónsson (1946) definitely records aneuploidy in the genus, although Gustafsson (1932) gives some counts as 2n=23-24 etc. it is not apparent whether this is a genuine record of an aneuploid chimaera, or merely an uncertainty as to the correct count. Earlier work, for instance Rosenberg (1909), often shows similar variation in chromosome counts ("2n=20-30!") which is definitely due to uncertain cytology. In later work, Takemoto (1954, 1960) and Hoy-Liu (1963) record the occurrence of aneuploid chimaeras in some species (see appendix 4), and Hoy-Liu, Fürnkranz (1963) and Mosquin and Hayley (1966) record cells of different ploidy levels in the same tissue. I have not found this last situation in my investigations. Sörensen and Gudjónsson, and Fürnkranz (loc.cit) both record diploid, triploid and aneuploid counts in different individuals of the same species, and this is a situation which I believe may be frequent in some areas (see Chapter 8), but chromosome counts on different levels of polyploidy in different individuals belonging to the same species are very rare. The only certain record of this seems to be counts of 2n = 24 and 32 for T.schroeterianum, and the same counts for T.maculigerum, although in the latter case, I am not certain whether

Gustafsson's plant was correctly identified as he places this characteristic member of the Spectabilia in the Vulgaria. The majority of species in which obligate apomixis is the rule are in fact very constant in chromosome number, and aneuploidy has only once ever been recorded at the tetraploid level or above (T.tundricolum), except in cases where the plant is known to have been of sexual origin.

At the triploid level, aneuploidy is sometimes rather frequent however. If we enquire into the causes of aneuploidy in Taraxacum, we are, like Gudjonsson, likely to come to the conclusion that this condition must arise as a result of an irregular mitosis or meiosis: As many triploid Taraxaca probably possess a very irregular female meiosis (see Chapter 8), it is likely that aneuploidy is a result of incomplete restitution after a very irregular, but synaptic female meiosis. Gustafsson (1934a) figures megaspores of aneuploid origin, and it seems likely that a large number of triploid embryos may not be euploid, but that only monosomic and above-triploid embryos are usually able to survive. In higher polyploids, the female meiosis is (always?) asynaptic, and in these circumstances, it is probable that aneuploid megaspores will be of a very much less frequent occurrence. Higher aneuploids of a sexual origin (Sörensen 1958) are perfectly healthy, so that the aneuploidy is not likely to be a disadvantage in these plants as it is in many sub-triploid aneuploids (Sörensen and Gudjonson 1946).

If we agree that aneuploids are likely to arise apomictically from plants with a synaptic female meiosis, we may then follow the argument presented in Chapter 8 in suggesting that these synaptic triploids may also

be capable of some reductional meiosis, which will result in diploid or near-diploid sexuals. It is thus possible that we are likely to find aneuploidy in conjunction with diploidy. However, it is clear that a population containing sexual diploids will contain a proportion of aneuploids through the fertilisation of haploid egg-cells with the irregular pollen of apomicts. My work indicates that these aneuploids will be sub-triploid (see Chapter 8), but Sörensen (1958) has shown that aneuploids of a higher chromosome number may result from the fertilisation of some unreduced egg-cells of monosomic triploid sexual aberrants. This phenomenon is clearly not of great importance however, and the offspring of such a cross will be near-tetraploid, a type of aneuploidy not yet found in the field. Therefore, whereas sub-triploid aneuploids may arise from sexual individuals, or from synaptic facultative apomicts, super-triploid aneuploids are only likely to arise from plants in the latter category.

Sörensen and Guðjónsson (1946) have very thoroughly investigated the occurrence of "primary" (2n=23) and "secondary" (2n=22) aberrants in 13 species of Vulgaria (although cytology is restricted to T.polyodon and T.laciniosifrons, it is clear from morphological data that these aberrants occur in the other species as well). Although they have shown (Sörensen 1958) that sexual diploids may arise through the fertilisation of the reductional egg-cells which seem to occur in one of the monosomic aberrants, they have no evidence that the female meiosis of the triploids is ever reductional. As the triploid aneuploid aberrants that they record arise at a very low rate (between 8.0 and 0.1% depending on the species, average 2.2%) it is probable that these aberrants arose through irregular

segregation in an asynaptic meiosis as recorded by Gustafsson, and that synaptic meioses were not found in the female organs of the eu-triploids, (irregular segregation due to the synaptic meiosis of a triploid, such as is discussed in chapter 8, is likely to give a much higher proportion of aneuploid progeny). These authors have also found that 2n=22 aberrants arise from triploids at a very low rate (less than 0.1%) but that they arise from the monosomics at a very much higher rate than the monosomics arise from eu-triploids. In fact the monosomic state seems to be more liable to produce further aberrants than the original triploids. As has been explained in Chapters 7 and 8, each of the different monosomics which can occur (8 in all) produce a different, readily recognisable phenotype in these species. Although I have not consciously noticed any of these phenotypes in the plants I have grown in experimental conditions, it is probable that I have selected against these aberrants at the seedling level, as I have tended to grow on the most developed seedlings (Chapter 2). Haglund (1947) has claimed to have collected recognisable monosomic aberrants in the field, and several plants which I have collected for the herbarium are probably monosomic. Although I have obtained chromosome counts of 2n=23 from seedlings on a number of occasions, the only case in which a 2n=23 plant has flowered is in the Palustria-species T.austriniforme. Herbarium material of this species in Herb.Cantab. and Herb.Kew. indicates that the species is uniform but whether it is uniformly monosomic, or whether the chromosome number does not have an appreciable phenotypic effect in this section is not known.

Sörensen and Gudjónsson also record 2n=25 and 2n=26 aberrants, but

do not state either the rate at which these aberrants occur, or whether they are morphologically separable. I have personally recorded plants of 2n=25, 26, 27, 28 and 2n=29. When these plants have come into flower, they have proved not to be deviant from the species to which they apparently belong, but in the majority of cases it is not yet clear whether this is because the species concerned always has an aneuploid number, or because the differing chromosome number is not having a marked phenotypic response. The super-triploid aneuploid counts are shown in Appendix 3. Only in T.lannylobum and T.polyodon do I have definite evidence that the phenotype is unchanged by above-triploid aneuploidy.

From my mass chromosome counts of Durham populations it is apparent that in some localities aneuploidy is much more prevalent than in others. Unfortunately, these plants have yet to flower, so it not yet possible to determine whether super-triploid aneuploidy has any phenotypic response, but examination of the mature rosettes suggests that a species will show an identical morphology with chromosome numbers between 2n=24-2n=29. Comparative counts in Durham populations are given in table 8. and photographs of aneuploid cells in photograph 10.

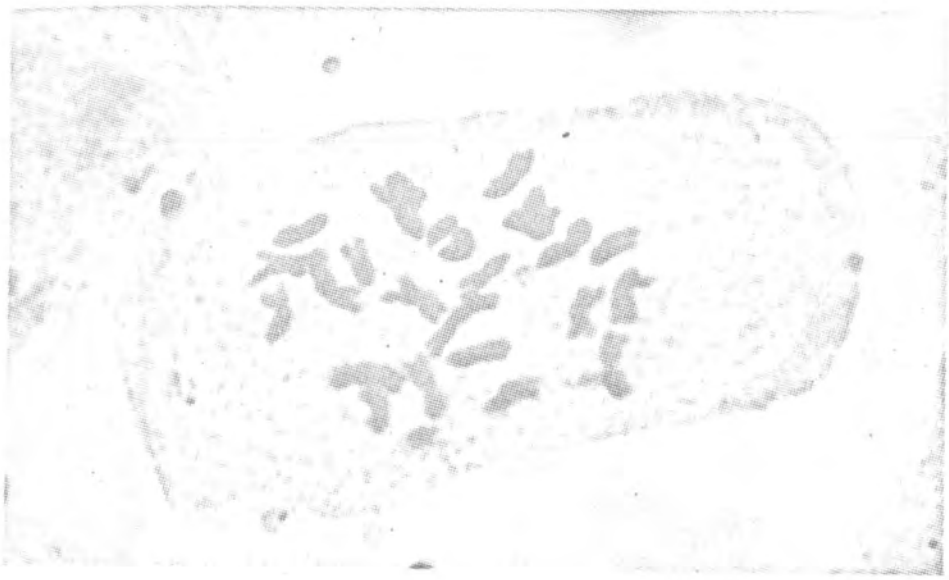
Table 8. Chromosome counts in Vulgaria populations in Co. Durham, showing the unequal distribution of aneuploidy

Locality	Species	2n=16	17	18	19	20	21	22	23	24	25	26	27	28	29
Thrislington-Ferryhill corner	T.sellandii									10					
Bishop Middleham Turn	T.cordatum T.sellandii									6					
Above Coxhoe	T.duplidens T.cordatum T.subcyanolepis									7		1			
Bishop Middleham quarry	T.sellandii									8		1			
Old Cassop	T.hamatum (and other spp?)									6	1		2		
Sherburn Village Corner	T.hamatum								1	5		3			
Sherburn House	T.duplidentifrous	1	1							12	1	2	1	3	1
										and one 2n=33					

The population at Sherburn Hill and Seaton Carew, both of which showed some aneuploidy are not included, as hybridisation between sections occurs at the former locality, and the taxonomic situation at the latter is very confused (see Chapter 11). In at least the former locality, we can suppose that a proportion of the aneuploidy is a product of pollination by apomicts onto sexuals (table 9).

Table 9

		2n=16	17	18	19	20	21	22	23	24	32
Sherburn Hill	T.subcyanolepis			2		2				15	(9 oxoniense)
Seaton Carew	T.lacistophyllum		1	1		1	1			15	(6 Specta-bilia)
	T.brachyglossum										
	T.unguilobum										
	T.maculigerum										
	T.hamatum										
	T.subcyanolepis										



Photograph 10. Aneuploid T. tanylobum, 2n-25.
Root-tip squash, with Feulgen staining.

x 3000

Conclusions from the chromosome counts of Durham populations:

There appears to be a much greater liability for aneuploidy to occur in some populations than others. There is some indication that when this aneuploidy is super-triploid that it may be associated with populations in which sexual plants are found, as these populations may have triploids with synaptic female meiosis which might be more liable to produce aneuploids. The Sherburn House aneuploids may be a case of this kind (diploids are found in this population).

It is not yet clear whether the various Vulgaria species differ in their ability to produce aneuploids, or whether there is any specific difference due to aneuploidy. That there is a difference between populations and that higher polyploids do not produce aneuploids seems beyond question.

Aneuploidy occuring in populations in which a fairly high percentage of sexual plants occur will be sub-triploid in the main, and will be caused by sexual, not apomictic means.

The 2n=33 plant at Sherburn House may be the result of an unreduced triploid monosomic sexual (elegans aberrant) crossed with n=10 pollen. This plant is healthy, and belongs to the Vulgaria. This tentative conclusion is reached because this is the only known case of a super tetraploid aneuploid and the only tetraploid Vulgaria yet known, apart from Guðjónsson's plants of this kind.

Sörensen and Guðjónsson (1946) mention that the commonest aberrant after triploid monosomics that they encounter are gigas 2n=48 aberrants. These might be formed either by mitotic restitution in the germ tissue of

the parents or by restitution in the homotypic phase of a restitutional heterotypic meiosis (giving a monad, as is frequently found in pollen formation in Taraxacum). They find that gigas aberrants arise in from 0.2-0.8% of triploids in 6 of the 13 species they worked with. As in the secondary aberrants, the monosomics give rise to gigas aberrants much more readily than the eu-triploids, these varying from 0.2-3.4% in 9 out of 10 possible aberrants in T.polyodon and T.laciniosifrons. These gigas aberrants are very readily recognised, and a number of authors have recognised gigas variants of various Vulgaria-species. I myself have several gigas specimens collected around Durham. I have not cultivated an entirely gigas plant, although I have observed gigas cells in T.pycnostictum and T.faeroense, both higher polyploids belonging to the Spectabilia, so the phenomenon is not restricted to triploids. The octoploid (2n=64) count recorded in T.shikotanense in the Ceratophora by Takemoto has not been included in Appendix 4, because it seems likely that this also was a gigas individual or tissue (this number has not otherwise been recorded for a Taraxacum species). The tetraploid cells recorded in the diploid species T.platycarpum, T.pumilum and T.wallichii doubtless arise in the same kind of way as gigas cells in apomictic polyploids, and indeed the first polyploids in the genus must have originated in a similar manner.

Cytological chimaeras

A certain amount of information on cytological chimaeras has already been given on the previous pages. It is clear that it is common to find more than one chromosome number in the root-tips of Taraxacum species. Table 10 tabulates the frequencies at which I have found the various types

of chimaera to occur.

Table 10. The Occurrence of cytological chimaeras in the Taraxaca I have examined

Total number of families on which chromosome counts have been made	Number of diploids/triploid families with chimaeras		Number of higher polyploid families with chimaeras
	Sub-triploid	Super-triploid	
349	8/234	4/234	5/115
	2.8%	1.4%	2.3%

Conclusions about cytological chimaeras:

They seem to occur in diploids and triploids (with some synaptic meioses) and higher polyploids (with asynaptic meioses) at roughly equal rates.

They may involve the gain or loss of 1-2 chromosomes, or they may be on different ploidy levels. The first type is rather more common.

There may be some tendency for a cell in an euploid tissue to lose chromosomes, rather than to gain them. This emphasises the fact that aneuploid cells occurring in euploid tissue will most usually be of mitotic origin, whereas aneuploid plants, which will be of meiotic, or less frequently mitotic origin, more frequently have extra chromosomes, not less.

Cytological chimaeras are not thought to be very important in Taraxacum, but their presence re-emphasises the care needed in all cytology.

Chapter 7

KARYOLOGY

Most cytologists who have worked on material belonging to Taraxacum have come to the conclusion that it is not possible to differentiate between the different somatic chromosomes arising at metaphase. Although Gustafsson (1932) professes to be unable to identify the chromosomes with certainty, he has deduced that some triploid species at least are of auto-polyploid origin from the idiograms which he has drawn. From this data, which is not published, he has been able to agree with earlier authors that the apomictic Taraxaca are of hybrid origin, and that the hybridity has itself been instrumental in initiating apomixis. In chapter 8, I have discussed this viewpoint in the light of more recent knowledge, and I have reached the tentative conclusion that hybridity has only given rise to apomixis, insofar that the meiosis of triploid hybrids is more likely to be unstable than that of autotriploids, and thus restitution will tend to occur in hybrids.

By far the most thorough karyological work in the genus has been performed by Gudjónsson (in Sörensen and Gudjónsson 1946) and it seems likely that in a work in which 8 different chromosome aberrants can be completely correlated with morphological variations in the gross structure of the plant, the results are likely to be very reliable. I quote (loc. cit. p. 32):

> "could hardly be identified with certainty, but by intensive work day by day during several months, and a minute study of hundreds of drawn plates, I gradually acquired such a knowledge of the different chromosomes, and their different modes of behaviour, that a reliable idiogram could be drawn."

Although I have had the additional benefits of modern cytological techniques (including the root-tip squash technique, and the aids of pretreatment), I have not felt able to tackle a task of this size during my research work, and the few idiograms that I have drawn are not of the accuracy that will result from experience and the examination of many plates. This is certainly due, I hasten to add, to my lack of endeavour - I am sure that many of my preparations are suitable for karyological analysis.

The only other karyological work in Taraxacum is that by Małecka (1962) and it is difficult to know how to comment upon this. It is unfortunately handicapped in that only the macrospecies names of Handel-Mazzetti (1907) are employed, and these are of very little systematic value (as I have argued at fuller length in chapter 9). The Polish workers cannot be entirely blamed for this however, as according to Professor Soest, I am the only person to have examined the Taraxacum flora of Poland since von Handel-Mazzetti, and only very briefly at that. We have no assurance that the meticulous precautions and careful endeavour of Gudjónsson was repeated by Mlle. Malecka, and from her results we can only suppose that this was the case. The microphotographs which are used as supporting evidence are of a very inferior quality indeed, but this may be a reflection on Polish printing, rather than the original cytology. It is very important to examine the reliability of Małecka's data very closely, because she directly refutes the conclusions drawn by Gudjónsson, and comes to the conclusion that many polyploid Taraxaca are of an allogamous origin. She is further unable to find the same genomic construction as

Gudjónsson, in any of the plants she has examined.

In table 11, the basic findings of Gudjónsson are summarised, and in table 12, those of Małecka are presented for comparison.

Table 11. The karyology of the species investigated by Gudjónsson (1946)

Species	2n=	A	B	C	D	E	F	G	H
T.obtusilobum	16	2	2	2	2	2	2	2	2
T.confertum	16	2	2	2	2	2	2	2	2
T.polyodon	24	3	3	3	3	3	3	3	3
T.laciniosifrons	24	3	3	3	3	3	3	3	3

Chromosome	Mean length	Constrictions
A	3.3	submedian primary, submedian secondary.
B	3.0	submedian primary, submedian secondary.
C	2.3	submedian primary, submedian secondary.
D	2.0	submedian primary, submedian secondary.
E	2.8	median primary, submedian secondary.
F	2.6	median primary, 2 submedian secondaries.
G	2.0	median primary only.
H	3.0	median primary, 2 submedian secondaries, satellites.

It should be pointed out that not only are the results in these 4 species the result of a very large number of examinations, but that there is considerable circumstantial evidence, and some actual karyology, that another 11 species in this section are similar in composition to T.polyodon and T.laciniosifrons.

Table 12. The karyology of species investigated by Malecka (1962)

Species	2n=	AB	CD	EF	G	H	"Type II"	
T.pieninicum	16	1	2	2	4	2	4	=15?!
T.laevigatum	24	3	3	3	6	3	6	
T.obliquum	24	3	3	3	6	3	6	
T.palustre	24	3	3	6	6	3	3	
T.palustre	40	5	5	10	10	5	5	
T.officinale	24	3	2	6	6	3	4	
T.officinale	24	2	4	8	6	2	2	
T.officinale	24	2	2	7	10	1	2	
T.alpinum	24	2	2	10	2	2	6	
T.alpinum	32	2	5	10	8	2	5	
T.alpinum	40	4	4	10	12	4	6	
T.nigricans	32	2	5	10	8	2	5	

Chromosome "type II" is 2.5 in length, and has one, sub-median constriction.

In none of the samples that Małecka examined was it possible to show an even distribution of Gudjónsson's karyotypes, and indeed, she was only able to recognise 6 basic chromosomal types. Even allowing that type II is equivalent to Gudjónsson's chromosome C, we are not able to find any evidence of autopolyploidy from these results. It has been pointed out however (Gustafsson 1947) that even an equal distribution of chromosomal type in the genome is not evidence of definite autopolyploidy, it being quite conceivable that different species or even sections might show the same karyology, despite the possible presence of translocations and inversions.

At this unsatisfactory state of affairs, we must leave past work in the genus with the knowledge that some species in the Vulgaria show 3 sets of individually distinguishable chromosomes, and that the chromosome complement of a genome is identical in diploid Vulgaria. Mlle. Malecka's results do not agree with this conclusion.

My results are tabulated below. These are very tentative, and are for the most part based on one metaphase plate only for each species. Photographs of these plates, and their interpretation is to be found in photographs 11-18.

Table 13. My own karyological data

Species	2n=	1=G	2	3=C	4=H	5	6=F	7=E	8	9
T.aurotinum	16	4				6	4	2		
T.bessarabicum	16					4	4	4		4
T.isophyllum	16	6	4		2				4	
T.viride x T.polyodon	17	9	5		1				2	
T.argutum	24	12			3		3		6	
T.hibernicum	24	12		6					6	3
T.bracteatum	24						3		15	
T.gulmargense	24	6	6	3	3	4	2			

The numbers at the top refer to my own chromosome numbering scheme. Where these seem roughly equivalent to Gudjonsson's chromosome types, this is indicated;

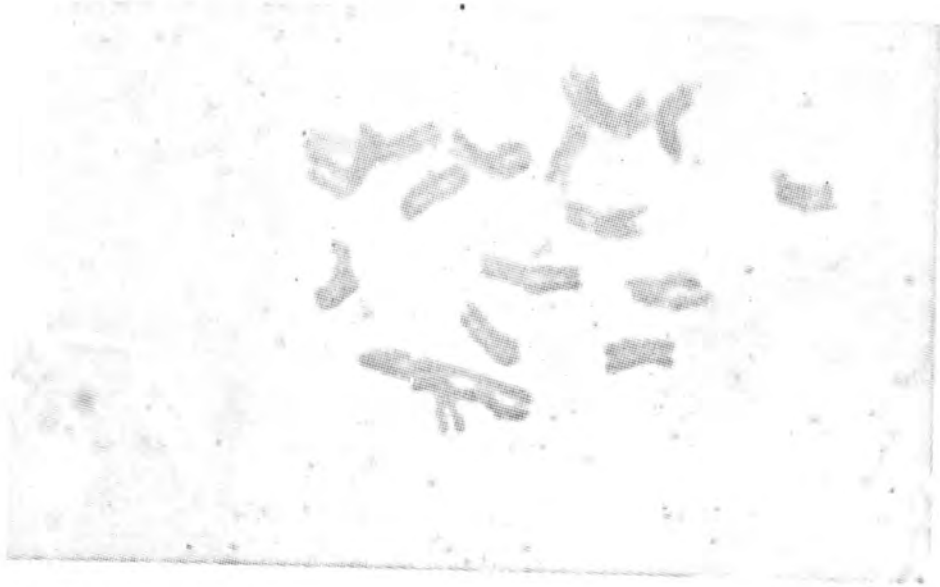
16 + 08

...ograph 11.

...marabicum, section Leptocephala

..., Cluj, Roumania, 1966.

...ot tip mitosis.



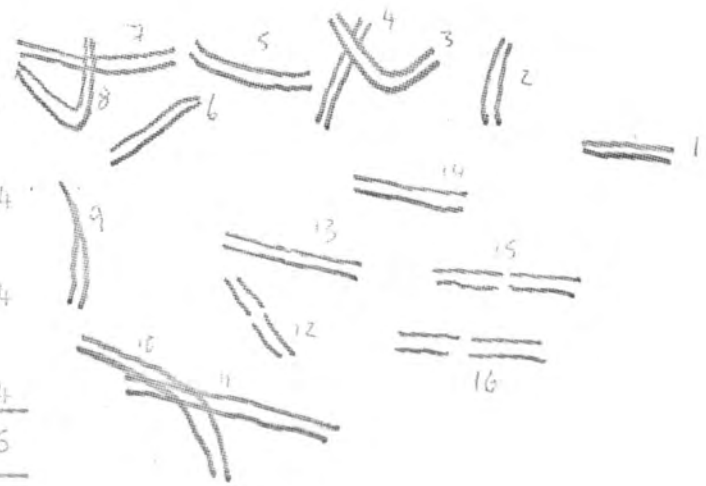
Type 'E', 2. Ou, median,
1, 6, 9, 16 = 4

Type 'F' 2. 5u, median,
2, 5, 12, 15 = 4

Type 'G' 3, Ou, median,
3, 8, 13, 14 = 4

Type 'I' 4, Ou, median,
4, 7, 10, 11 = 4

16



446

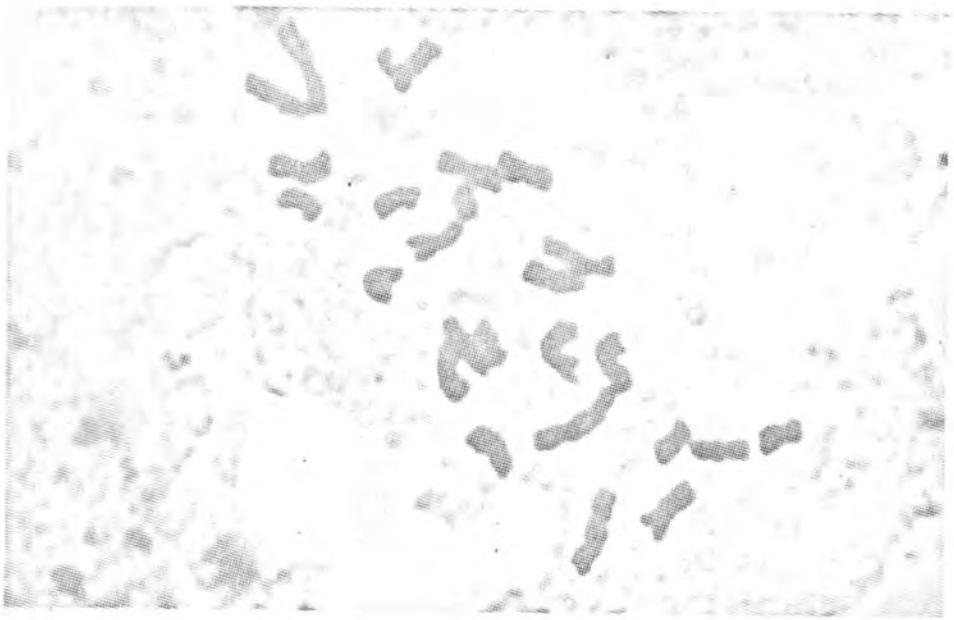
24 + 3S, 1B

Photograph 12.

T.argutum. Section Erythrosperma.

Ex.Strathtummen, Perth. 6-1965

Root-tip mitosis



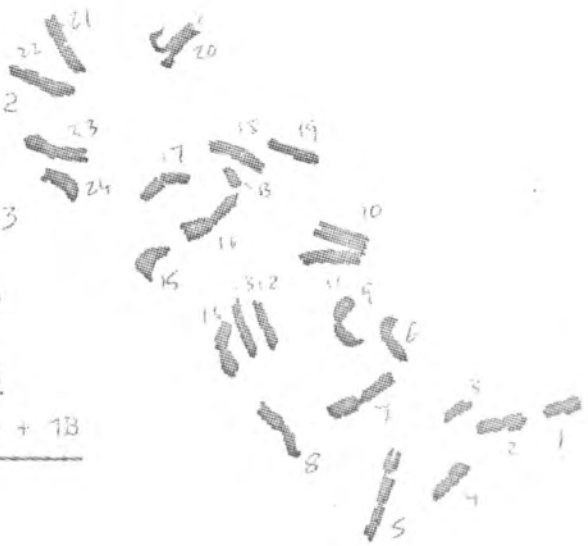
Type 'A', 1.8 u, median,
2, 4, 6, 8, 9, 11
13, 14, 16, 18, 19, 23. = 12

Type 'D' 1.8 1. 0u
satellite.
5, 7, 21 = 3

Type 'F' 2.5 u, median
10, 20, 22 = 3

Type 'H' 1.2u, median
1, 3, 12, 15, 17, 24 = 6

24 + 1B



16 + 28

Photograph 13

T.isophyllum ex. Kovaskovska, C,S,S,R. 5-65
Section Erythrosperma. Root-tip mitosis.

Type 'A', 1.8 u, median
3, 4, 7, 11, 14, 16 = 6

Type 'B', 1, 5 u, median,
5, 6, 10, 13 = 4

Type 'D' 1.8 u + 1.0 u
satellite
2,9 = 2

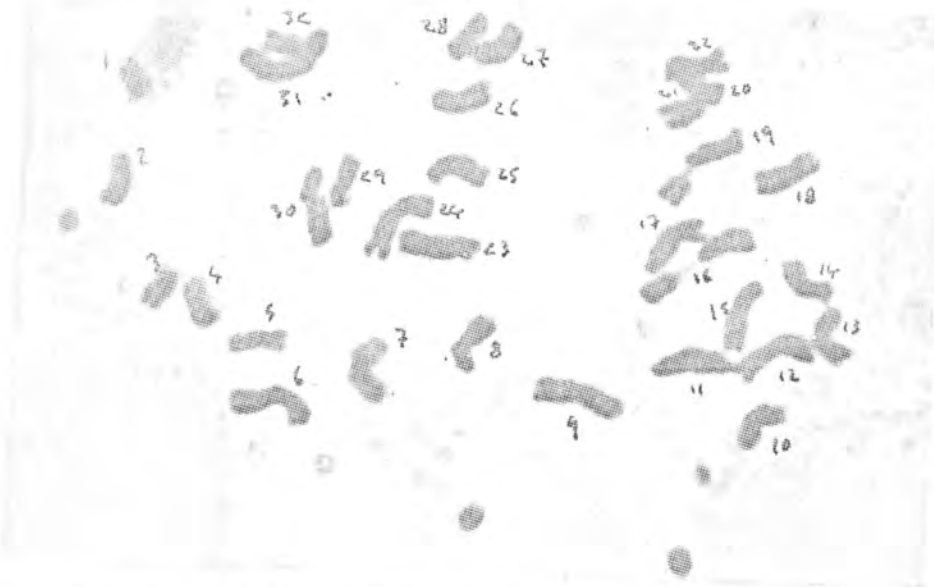
Type 'H', 1.2 u, median
1, 8, 12, 15. = 4

16 + 28

Photograph 14

32 + 28

[illegible] Harmonii. Section Spectabilia.
[illegible]. Langdon Beck, Durham, 6-1965
[illegible]-tip mitosis

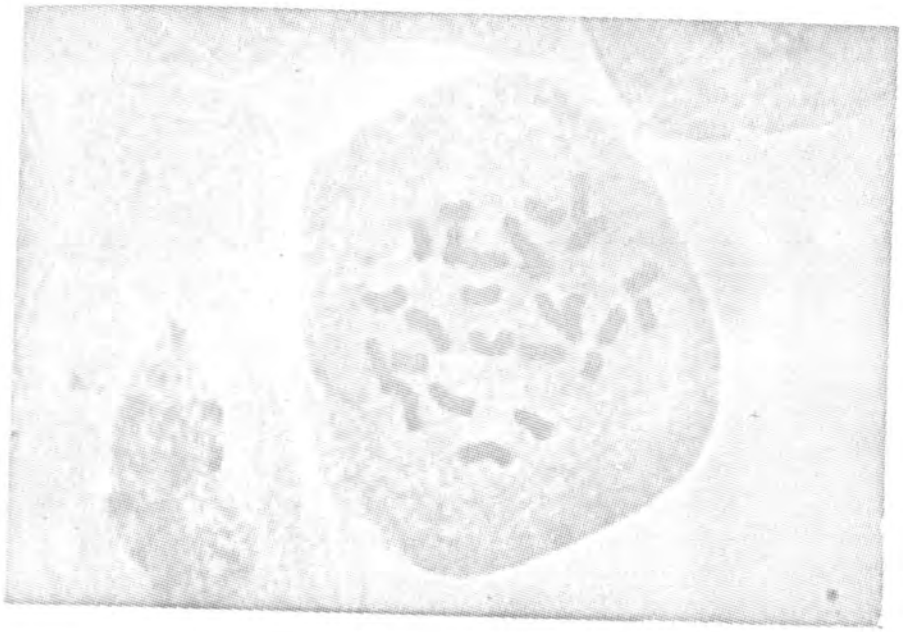


Type 'A' or 'E' 1.8-2 Ou, median
5, 10, 13, 14, 18, 25, 26, 32 = 8
Type 'B' 1.6u, median
2, 4, 20, 22, 27, 28 = 6
Type 'D' 1.8 u + 1.0u satellite
16, 19 = 2
Type 'F' 2.5, median 8, 11, 15, 17
u 23, 24, 30, 31 = 8
Type 'G' 2.8 u, median
6, 7, 9, 12 = 4
Type 'H' 1.2 u, median
1, 3, 21, 29 = 4
32

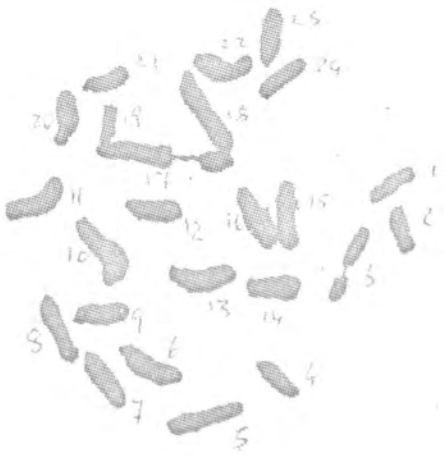
24 + 38

Photograph 15

...sulmargense, section Kashmirana.
Ex. Kashmir, J.L. v.S. 1964
Root-tip mitosis. .



Type 'A'	1.8u, median 1, 9, 11, 15, 22, 24	= 6
Type 'B'	1.6u, median 2, 4, 12, 19, 20, 21	= 6
Type 'C'	2.2u, sub-median 7, 8, 12	= 3
Type 'D'	1.8u + satellite 0.8u 3. 16. 17	= 3
Type 'E'	2.0u, median 5, 6, 13, 14	= 4
Type 'F'	2.5u, median 10, 18	= 2
		24

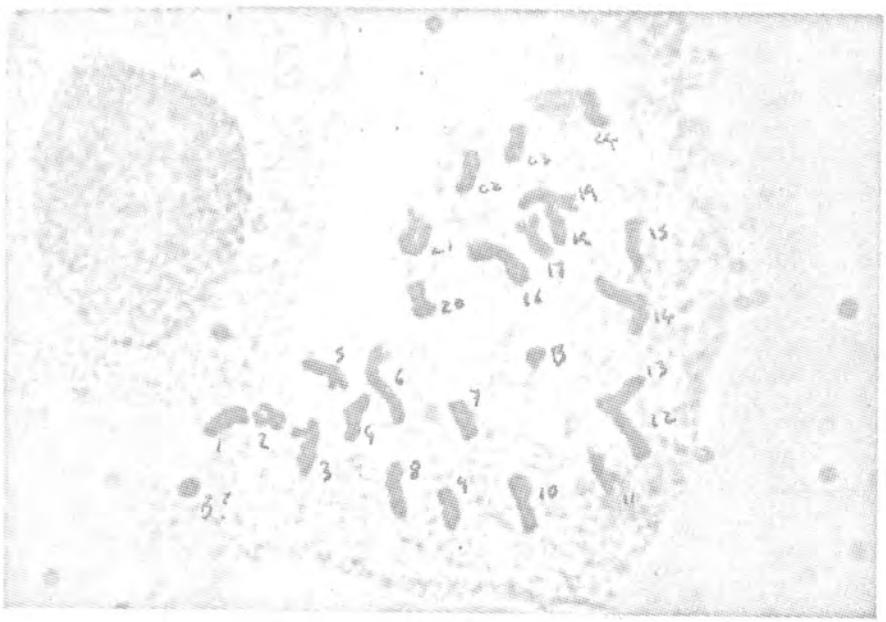


Photograph 16 — 24 + 1B

S. hibernicum. Section Spectabilia.

Loc. Fen near Kirriemuir, Angus, 6-1965.

Root-tip mitosis



Type 'A' 1.8u, median
1, 4, 5, 7, 9, 11
13, 17, 18, 22, 23, 24 = 12

Type 'C' 2.2u, median,
8, 10, 12, 15, 19, 3 = 6

Type 'H' 1.2 u, median
2, 20, 21 = 3

Type 'I' 3.5-4.0 u median
6, 14, 16 = 3

24 + 1B

16 = 03

Photograph 17

Lycopersicum, section Serotina.

Iași, Roumania, 1964

Pre-tip mitosis

Type 'A' 1.8u, Median
1, 4, 10, 16 = 4

Type 'E' 2.0u, median
2, 3, 5, 8, 12, 14 = 6

Type 'F' 2.5u, median
6, 7, 9, 15 = 4

Type 'G' 2.8u, median = 2

16

Photograph 18

17 + 1S

F1, T.viride, section Fontana, 2n=16 x
T.polyodon, section Vulgaria, 2n=24
Root-tip mitosis

Type 'A' 1.8 u median
2, 3, 5, 9, 10, 11, 15, 16, 17 = 9

Type 'B' 1.5 u median
1, 6, 8, 12; 13 = 5

Type 'D' 1.8 u + satellite 1.0 u
4 = 1

Type 'H' 1.2 u median
7, 14 = 2

17 + 1S

1,2.0	, median	= G?
2,1.5	, median	= ?
3,2.2	, sub-median	= G?
4,1.8	+ satellite, 1.0	, median = H
5,2.0	, median	= ?
6,2.5	, median	= F?
7,2.8	, median	= E?
8,1.2	, median	New?
9,4.0	, median	New?

The following conclusions can be drawn from this work:

Only 5 out of the 9 chromosome types which I recognised are referable to earlier work (especially Sörensen and Gudjonsson 1946).

The chromosome type 9 and 8 are respectively larger and smaller than others noted before.

The distribution of various types is very uneven in some species.

Only chromosome E showed a sub-median constriction, rather than a median one.

The constrictions were often very hard to determine, and this may be a major contributing factor to the evident unreliability of these results.

The other main reason why the results are disappointing is that they are only taken from one (or at the most 3) metaphase plates per species.

There is some indication that karyology of Taraxaca may be unreliable in any case, except perhaps when taken from large samples. Perusal of Appendix 4 will show that the number of satellited chromosomes, which are very readily recognised, is very variable, between species, between families inside a species, between siblings, and even in the same individual. Presence

of satellited chromosomes seems to be uncorrelated with any known factor, although it may be a consequence of the fixing or hydrolysing techniques, as may the greater variability in chromosome size found in the plants I examined compared with those examined by the earlier workers. In point of fact, it might be possible to obtain comparable results using the forms of fixing, staining and sectioning used by Gudjónsson and by Małecka (Navashin's Fixative with Karpetchenko's modification, with staining in Gentian Violet). This has not been tried.

Satellited chromosomes are only found in the more advanced sections and this has been used as evidence in determining evolutionary pathways in the genus 12. In the pentaploid and hexaploid Spectabilia and Palustria they are not found, and indeed they are very unusual in these sections. The Erythrosperma and Vulgaria usually do show some satellites, but these rarely are of a constant number, equal to the level of polyploidy.

1-2 supernumerary chromosomes are found in some species. An example of a species with one is T.hibernicum (photograph 17). B chromosomes may be characteristic for some species, but there is evidence that the number that will be found is variable (again see Appendix 4 for further information).

Chapter 8

SEXUALITY AND AGAMOSPERMY

The earliest reference to agamospermy in Taraxacum seems to have been by the Swede Murbeck (1904). Papers by Juel (1905), Ikeno (1910), Osawa (1913), Sears (1917, 1920) Schkorbatow (1912), Rosenberg (1909), Stork (1920), and Gustafsson (1932a, 1933, 1934, 1935a, 1935b, 1947) confirm this behaviour and greatly increase our knowledge into the occurence, mechanism and cytology of this agamospermic genus. Later papers by Poddubnaja-Arnoldi and Dianova (1934), Poddubnaja-Arnoldi (1939), Haran (1952, Małecka (1958, 1962) and Sörensen and Gudjonsson (1946) further increase our knowledge about the Karyology, Aneuploidy and occurence of the agamospermic species, but by 1935, the mechanism of agamospermy was already rather thoroughly known. The embryological information is summarised in Chapter 3. Perhaps the most outstanding feature of the combined work were the repeated findings that all agamospermic species were polyploid (most commonly triploid, but also tetraploid, pentaploid, hexaploid, with one recorded octoploid, Takemoto 1954.)

The first diploid sexual Taraxaca were found by Gustafsson (1932) who found diploids in the Scariosa (T.minimum), Serotina (T.serotinum), Leptocephala (T.bessarabicum), Mongolica (T.platycarpum) and Vulgaria (T.confertum). Shortly afterwards, Poddubnaja-Arnoldi and Dianova (1934) found several diploid sexual species in Asia, namely T.kok-saghyz, T.multiscaposum, T.monochlamydemeum (Macrocornuta) and T.nutans (?Calanthoidia). These findings established the occurence of diploid

sexuals in the Mediterranean and Asia, and further papers by Gustafsson (1937) and Małecka (1961) described the occurrence of totally diploid sexual species in northern Europe (T.obtusilobum and T.pieninicum). Both species are in otherwise agamospermic sections (Vulgaria and Eu-Erythrocarpa respectively). Further, Holmen (1952) found that T.pumilum (Laevia) from Greenland is also a diploid sexual species . My work has found a number of other diploid sexual species, namely T.kotschyii (Rhodotricha), T.stevenii (Orientalia), T.oliganthum (Oligantha), T.leucanthum (Leucantha), T.haussknechtii (Serotina) and T.bithynicum (Scariosa), all Asian, and T.viride (Fontana) in the Alps. Hoy-Liu (1963) also gives a number of diploid species from Asia, namely T.elegans, T.fulvo-brunneum (Kashmirana), T.heyboekii (Tibetana), and T.wallichi (Macrocornuta). I have also found diploidy in the last species.

To sum up, most of the Asian sections have been shown to contain at least some sexual species. It is thought (Chapter 12) that the 5 most 'primitive' sections in the genus, found in the Near-East, are entirely sexual. Other sexual species are found in largely agamospermic sections both to the east and the west of the presumed centre of origin of the genus, some occurring in apparently highly 'advanced' sections (e.g. the Vulgaria). Nevertheless, the vast majority of Taraxacum species are thought to be totally agamospermic. To date, the chromosome numbers of 156 Taraxacum species are known (see appendix 4). Of these, only 23 (14%) are totally diploid and sexual. This is almost certainly an over-estimate, as those sections with the most species (Vulgaria, Spectabilia, Ceratophora and Erythrosperma) have very few sexual species (only 3 known altogether). It

is probably true to say that less than 5% of the total number of species are wholly sexual.

In 1949 came the first hint that the distinction between sexuality and agamospermy is not so clear-cut as had previously been thought. Tschermak-Woess discovered a number of sexual individuals in the region of Vienna, and showed that they were all diploid. Most interesting, sexuals were found in no less than 5 macrospecies, which can be taken to belong to 3 different sections (see chapter 9). This work was followed by Fürnkranz who has conducted a lengthy investigation in the Vienna area (1960, 1961, 1965). Briefly, Fürnkranz found that varying proportions of populations were diploid and sexual, up to 70% sexuals being found in the Erythrosperma, but the proportions were very variable, and many populations had fewer, or no sexuals. Fürnkranz discovered that it is possible to determine the chromosome number of an individual through the examination of its pollen (discussed later in this chapter). He also found that intersectional hybridisation was found in the field and could be readily induced in the laboratory (chapter 9) and that apomictic pollen crossed onto a sexual segregated sexual and agamospermic offspring; usually, but not always depending on the chromosome number of the offspring (also discussed later in this chapter). We suspected from Fürnkranz's results that a polymorphism for sexuality and apomixis might be occurring in the Vienna populations, with sexuals giving rise to agamospermic individuals through pollination with agamospermic types and that these might revert to sexuality through facultative agamospermy. This seemed the only hypothesis, however unlikely, that would account for sexual and agamospermic individuals of the same species

(apparently) occurring in the same populations with different chromosome numbers correlated with the breeding behaviour. This last condition seemed to rule out the possibility of sexuality or agamospermy governed by climate or light regime, as is found in some grasses, while the maintenance of two autonomous lines of the same species, with different chromosome number and breeding behaviour (as is found in Poa, Cardamine etc.) seemed unlikely in view of the ability of the agamospermic plants to fertilise the sexuals. The sexual line would soon have been hybridised out of existence if there was no possibility of sexuals arising anew from the apomicts. That the two types occurred in the same locality, and seemed to belong to the same species precluded the possiblity of a physiological (as in Hieracium of different species) or geographic (as in Antennaria) breeding barrier. A polymorphism seemed a possibility, but this invoked a facultative apomixis in the triploids, which had only been reported once before in Taraxacum, by Sörensen (1958) as a very rare condition, although Fürnkranz (1961) claims to have observed it in tetraploids without recognising the significance of the observation.

The work of Sörensen is of a very different nature, and although it seems to be less important in order of magnitude in causing the occurrence of sexuality into populations, it is nevertheless of such extreme interest that I am discussing it fully. In an earlier paper (Sörensen and Gudjonsson 1946), the occurrence karyology and morphology of a complete series of triploid monosomic aberrants is reported for a number of species in the Vulgaria. This is discussed in chapters 6 and 7. In the second paper, Sörensen reveals that of the eight possible aberrants in T.polyodon,

T.cordatum and T.laciniosifrons, two show some sexuality. Aberrant tenuis seems capable of reproduction only by the fertilisation of wholly reduced egg-cells. Aberrant elegans shows only unreduced (restitutional) egg-cells, but the chromosome numbers and morphology of crosses made onto this aberrant show that it is capable of both agamospermic and sexual reproduction. The progeny of the hybrids made onto the unreduced egg, are naturally approximately tetraploid (n=23 x n=8-10). As these aberrants arise at between 0.05 and 0.1% per generation, it is clear that they cannot have a very significant part to play in wild populations, particularly as both aberrants are weak, and may not be able to survive any competition. In fact, the greatest praise is undoubtedly due to the authors of this very elegant work in detecting the aberrants at all, let alone of determining their reproductive behaviour. The results of the work as summarised above do lead to an interesting conclusion. The aberrant elegans shows no female meiotic reduction, and yet it is capable of some sexuality, which the rest of the polyploid apomicts apparently are not. Clearly there is a control determining whether a plant shall be agamospermic or sexual, which is independant of the female meiosis. As we have seen that agamospermy in Taraxacum results in the production of precocious embryos, it is possible that this control determines whether the embryo develops before anthesis, or only after fertilisation. If the embryo does develop precociously, we can assume that sexuality is impossible.

Yet in aberrant tenuis, of the same species, the egg-cell is invariably a result of a complete meiotic reduction, and is never capable of developing autonomously. Agamospermy has yet to be recorded in a Taraxacum plant with

less than 2n=22. It seems to me that two basic principles of Taraxacum reproduction can be inferred from these data:

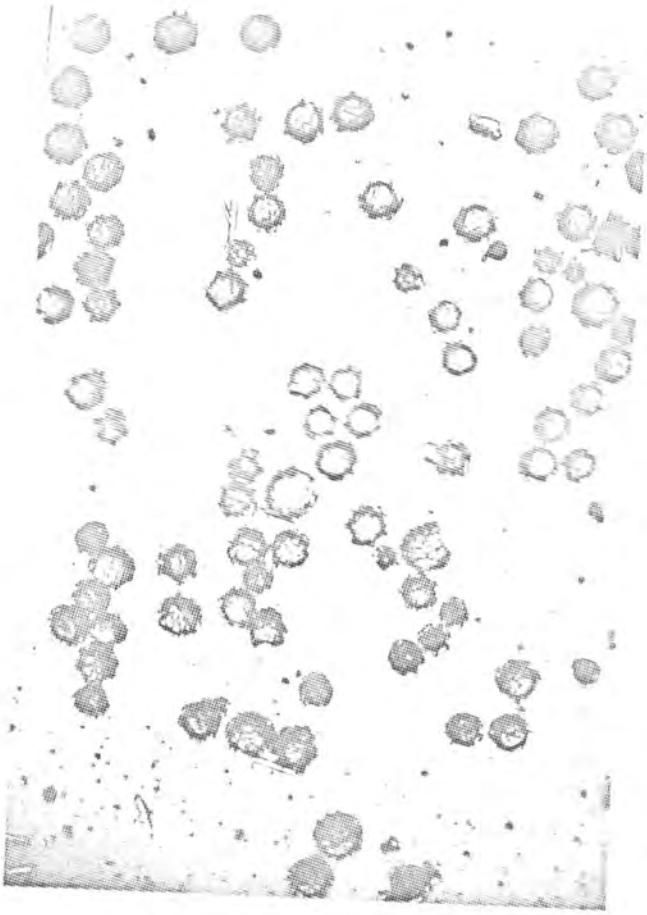
1. The meiosis and embryo development of the plant are independent, and in any system ensuring agamospermy, control of both restitution in female meiosis and precocious embryo development is necessary.
2. Control of meiotic reduction seems to be on chromosome H, which is only present twice in abb. tenuis. Control of precocious embryo development seems to be on chromosome D which is only present twice in abb. elegans. To my mind, a reduced egg-cell seems to ensure that the embryo does not develop before anthesis (as no diploid apomicts have ever been found), and therefore the sexuality of abb. tenuis is a product of a reduced egg-cell, rather than an effect of the missing chromosome H on precocious embryogeny.

It should be noted that none of these tentative conclusions drawn from the papers of Fürnkranz or Sörensen have been made by the authors themselves and any of these comments seemed good leads for future work, rather than definite conclusions. But a link had emerged which seemed to join the two apparently distantly related problems of these two authors. This link is the obvious, but seldom commented upon question of the restitution or reduction of female meiosis. It was in the control of female meiosis that I felt the key to the question of the origin and control of agamospermy lay.

It was necessary in the first place to obtain material from populations in which both diploid sexuals and triploid agamospermic plants occurred together. During the first summer of my work, I collected pollen samples

(by fixing unopened heads in 3.1 acetic-alcohol) from many sites throughout Britain, and later examined the pollen in the laboratory. Fürnkranz reported (1960) that all diploid sexuals have regular pollen, and all apomicts have highly irregular pollen, or no pollen at all. It therefore seemed that examination of the pollen should give a good idea where sexual plants were to be found, and indeed that pollen regularity might be as definitive a technique as Fürnkranz claims. In fact, the examination of the pollen of plants of known chromosome number showed that whereas Fürnkranz's technique is an oversimplification of the problem, at least when applied to British populations, it is possible with experience to detect the presence of sexuals in populations.

The pollen of Taraxaca can be divided into three main types. Most (all?) tetraploids have a large proportion of pollen grains of considerable size (35-45 microns diameter). These grains can be shown to be diad, that is to say the product of a restitutional male meiosis (photograph 19). The percentage of diad grains in these plants can vary between 50-60% (T. oxoniense, which is able to fertilise diploid plants with reductional pollen) to 100% (T.naevosum a triploid, as well as several tetraploid Spectabilia). All pentaploids, and a number of tetraploids (about half the species examined) have no pollen at all. Many triploids have pollen which is clearly the product of a rather irregular reductional male meiosis, and this can be shown to be so, the grains originating from triads, pentads, hexads, and the majority from tetrads. This pollen is rather regular, but the difference in the sizes of the grains, which vary from 15-30 microns diameter, with a proportion of very small (5-15 microns diamater) grains



Photograph 19. Diad pollen. T.naevosum

x 1200

Photograph 20. Irregular reductional pollen. T.subcyanolepis.

x 600

resulting from micronuclei, is still distinctive. Unfortunately, this type of pollen tends to grade imperceptibly into regular pollen with a diameter of about 25 microns which is characteristic of the diploid plants found in agamospermic populations. Experience has shown that only those plants with absolutely regular pollen can be safely determined as being from a diploid. The diploids T.serotinum and T.pieninicum would clearly not be detectable by this technique, as they both have irregular pollen resembling a triploid, resulting from an unexpectedly irregular male meiosis (Małecka 1961, 1965), but all diploid species in which I have examined the male meiosis and pollen show both to be very regular. (Photographs of regular and irregular pollen in photos 20-21). For discussion of the significance of the various types of male meiosis, and their analysis, see below.

In all, 195 populations in 31 vice-counties ranging from Hampshire to Sutherland have been examined for regular pollen. In all, some 1500 plants have been examined. Regular pollen has been found in 14 populations, (7%), at proportions varying between 75 and 5%. The distribution of these plants is shown in diagram 8. Owing to the rigorous exclusion of all plants which showed any irregularity of pollen, it is possible that these figures are an underestimate. Although pollen regularity can provide a useful guide to the breeding behaviour of Taraxaca, it is clearly insufficient to rely entirely on this evidence. In support, 278 chromosome counts have been made on seed collected in the wild in Britain. This was cytologically examined just after germination, as described in Appendix 1, grown to maturity, and the breeding behaviour and gross morphology carefully studied of the adult plants. The results of the

Diagram 8.

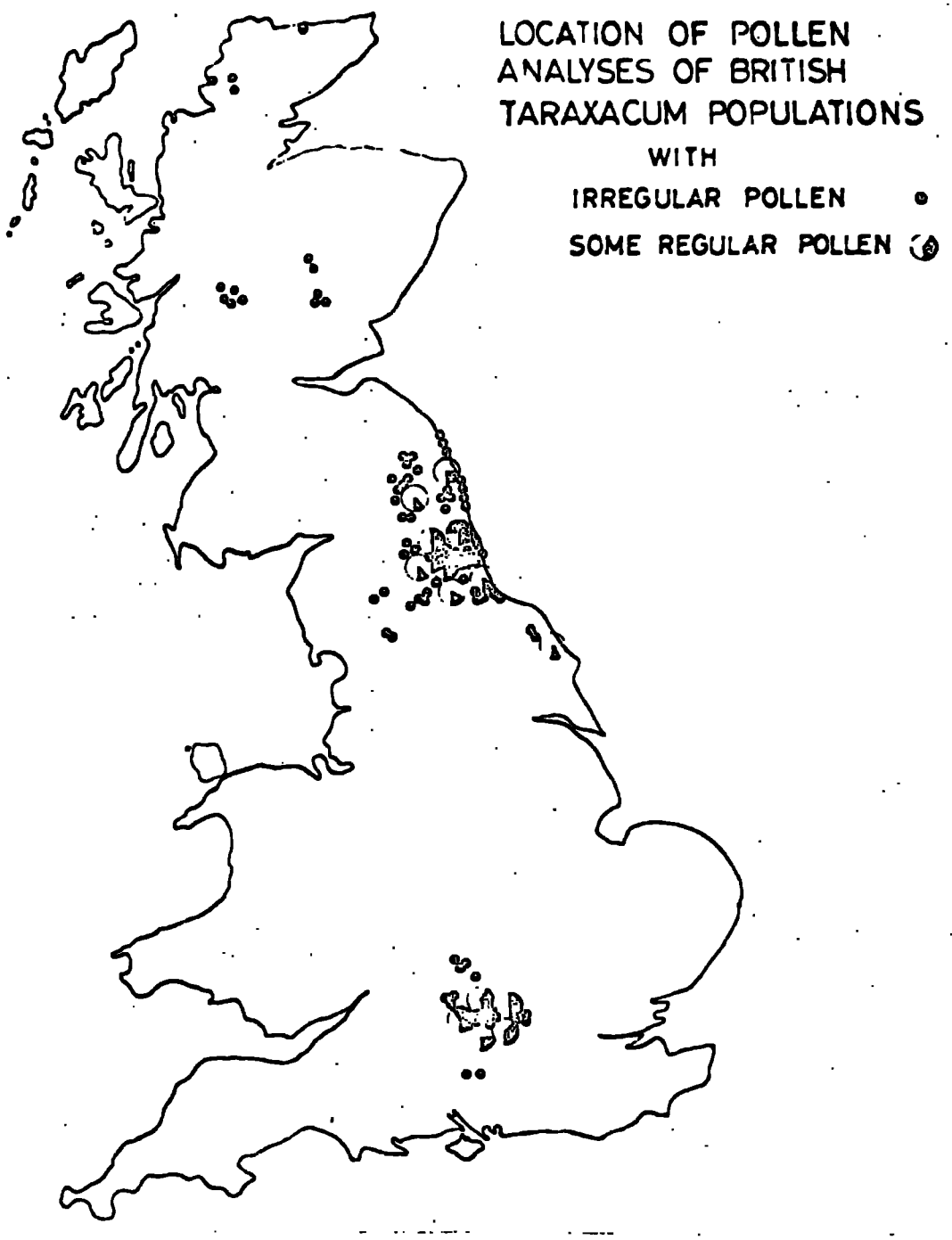
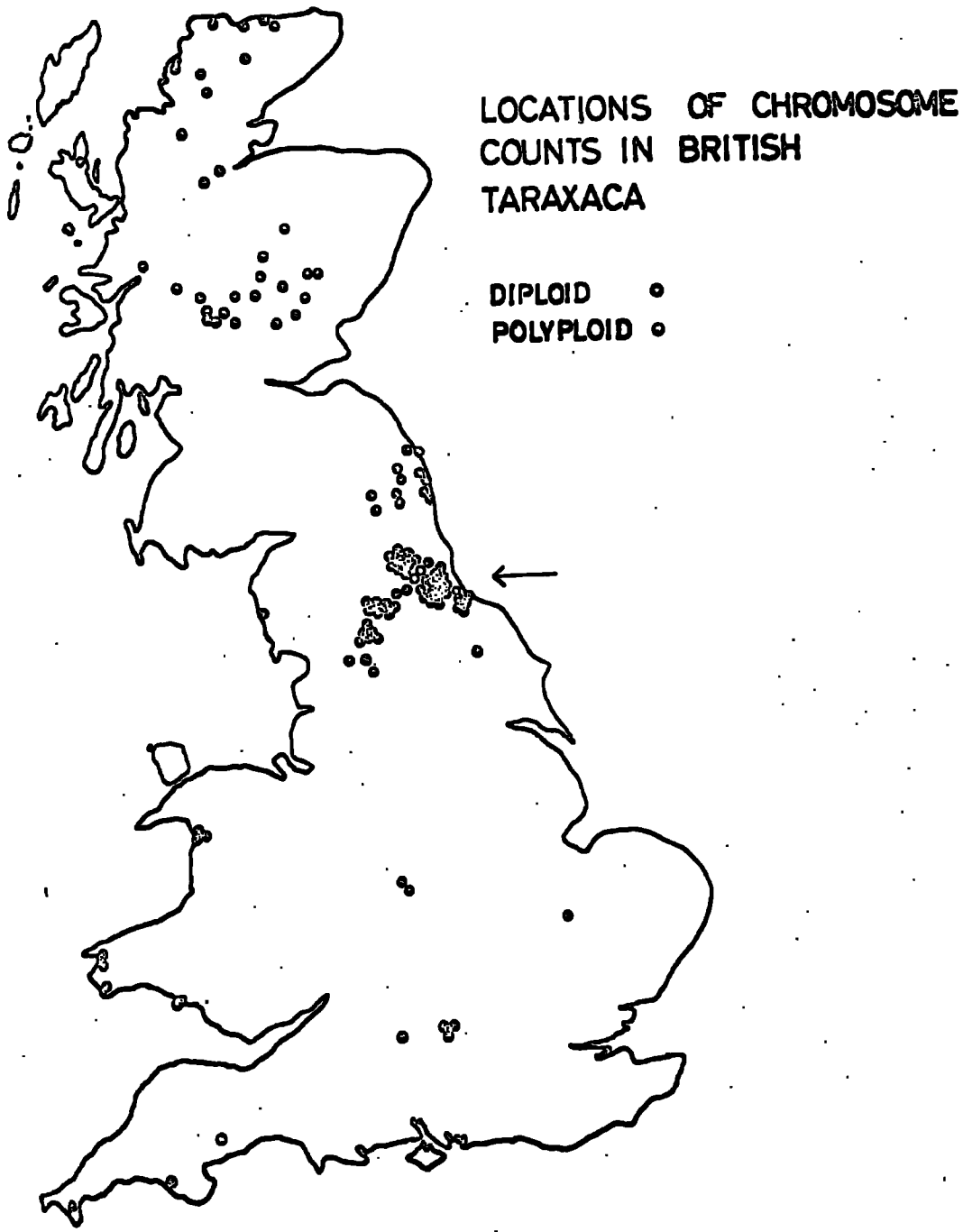

LOCATION OF POLLEN
ANALYSES OF BRITISH
TARAXACUM POPULATIONS
WITH
IRREGULAR POLLEN
SOME REGULAR POLLEN

Diagram 9.


LOCATIONS OF CHROMOSOME COUNTS IN BRITISH TARAXACA
DIPLOID
POLYPLOID

cytological examination is tabulated in detail in appendix 3, but they are summarised below in table 14.

Table 14. Chromosome counts in British Taraxaca

Chromosome count	2n=16-18 Always sexual	2n=24 Pollen reductional Usually apomictic	2n=24 Pollen restitutional, always apomictic	2n=32 Pollen absent Pollen absent or restitutional, always apomictic	
Number	10	712	8	88	Total:278
Percentage of total	3.6	61.8	2.9%	31.7	

Of the 182 plants with reductional pollen, triploids or diploids, 10, or 5.5% are diploid. From pollen examinations of populations in the field, about 7% had regular pollen. This included restitutional plants, which formed some 10% of all plants for which pollen examination in the field was made. Therefore the percentage of plants with reductional pollen which showed regular pollen is 8% This is not statistically separable from the percentage of diploid plants of 5% obtainable from chromosome counts.

The diploid plants belong to the species T.austriacum and T.brachyglossum (Erythrosperma) and T.polyodon and T.subcyanolepis (Vulgaria), but there is no indication that sexuality is likely to be restricted to these species. All the diploid plants have been found in lowland Co. Durham, but in view of the fact that plants with regular pollen have been found elsewhere in the country, and that over 70% of the plants with reductional pollen of which the chromosomes have been counted originate in Durham, it

is not thought likely that sexuality is restricted to this county.

The percentage of diploid plants in populations which have been cytologically examined, varies from 0-14%. This is nowhere as high as the proportions discovered through pollen examination, and this is thought to be due either to the bad seed-set of many sexuals, so that a lower percentage of the seed-heads collected would be sexual, or due to the earlier flowering of the sexuals. Fürnkranz reports that the sexuals in the Vienna area flower up to a week earlier than the bulk of apomicts. I fixed flower-heads for pollen examination about a month earlier than the dates on which I collected achenes for chromosome counts (the respective dates were 4-4-1965 to 11-5-1965 for pollen, and 27-5-1966 to 6-6-1966 for cytology). It takes between 12 and 18 days for seed to set, so about 7-14 days difference in flowering time is represented by the two collections.

The Durham populations may contain a considerable quantity of sexual plants, and this may be true of triploid Vulgaria and Erythrosperma throughout Britain and indeed western Europe (although perhaps not in Scandinavia, where there have been extensive cytological investigations by Gudjónsson and Gustafsson without finding any sexuals apart from the wholly diploid T.obtusilobum).

Although Fürnkranz was unable to supply me with material from the Viennese populations, and Sörensen had ceased to work on the monosomic sexuals, I was luckily able to obtain at an early stage in my studies material from Czechoslovakia of an essentially similar nature to that of Fürnkranz. In the spring of 1965, Professor Valentine very kindly collected a quantity of achenes from south-facing limestone slopes at Kova-

cover Kopce and Hlohovec, C.S.S.R. These plants mostly belong to the Erythrosperma (one Vulgaria and one hybrid).

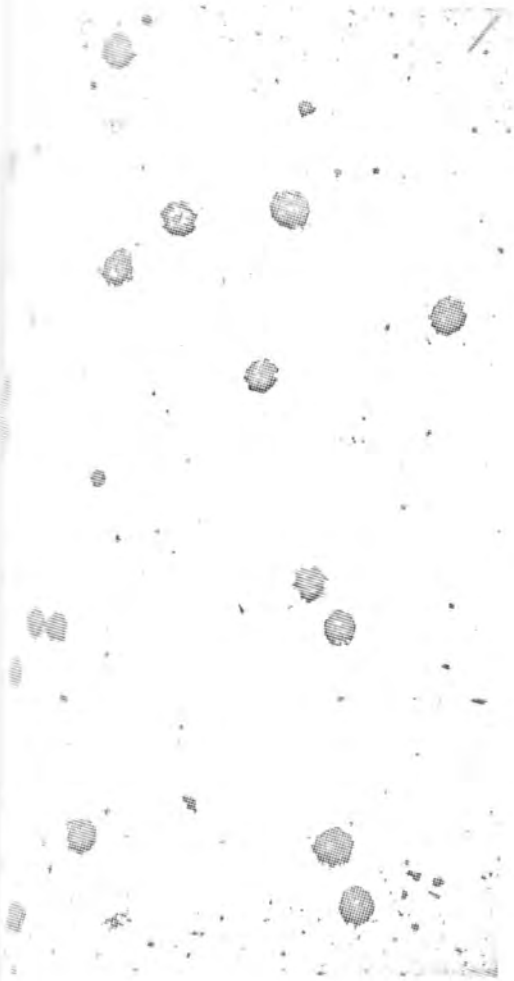
The majority of the plants collected from Kovacover Kopce, and from Hlohovec proved to belong to the Erythrosperma-species T.isophyllum Hagl. There were also one seed collection of T.austriacum v.S., belonging to the same section, and one seed collection of a plant which seems to be a hybrid between T.isophyllum and a Vulgaria-species. The chromosome counts and breeding behaviour of these collections are summarised in table 15.

Table 15 Summary of the chromosome counts and breeding behaviour of plants grown from seed collected at Kovacover Kopce and Hlohovec C.S.S.R

2n=	16	17	18	19	20	21	22	23	24
T.isophyllum	6					1			5
T.austriacum		1							
Hybrid	1* Sexual								1* Agamospermic

* Both chromosome numbers were found in different individual from the same seed head. The diploids were sexual, the triploids apomictic.

Both T.isophyllum and T.austriacum seem to be restricted in distribution to regions of central Europe. One individual of T.austriacum has been found growing in clinker at the dock-side at Haverton Hill, Middlesborough, England, and it seems almost certain that this was an alien. It was diploid 2n=16, and sexual. It is difficult to know whether T.austriacum is always sexual, as only two seed-heads have been examined. It seems likely that in these populations at any rate, sexual and apomictic



Photograph 21. Regular reductional pollen . T.brachyglossum. Thrislington, Co. Durham.

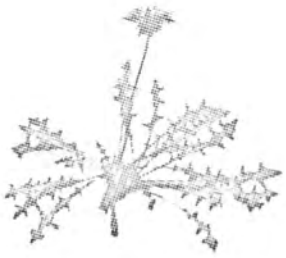
x 600

Photograph 22. Herbarium specimen of cultivated T.austriacum; diploid sexual. Haverton Hill, Co. Durham (as an introduction).

x 1/4

individuals of T.isophyllum occur together, possibly in roughly equal proportions. Whether this is true of this species throughout its range is not known, and indeed, this is a very tenuous conslusion to draw from 12 seed-samples from two different localities. What is needed is a much more thorough investigation on the site, and I am going to carry this out in the summer of 1968. It is not yet clear whether the high rates of sexuality that Fürnkranz reports in 'T.laevigatum' might refer to this particular species, or whether, as Fürnkranz's data seem to suggest, sexual diploids appear at a high frequency in several central European species, a phenomenon which does not apparently often occur in Britain. The possible reasons for this are discussed later.

The diploid and triploid T.isophyllum were grown to maturity in standard conditions of light and heat, as is described in chapter 3. When these plants flowered, it became apparent that the diploids could not be separated from the triploids on any morphological characteristics, save that the triploids were a little bigger. Photographs of herbarium specimens of diploid and triploid T.isophyllum from Kovacover Kopce appear as photographs 23 and 24. Professor van Soest, the Taraxacum authority, saw all my material from this locality, and agrees with me that the diploids and triploids are without doubt referable to the same species. When this material fruited in the insect-proof greenhouse, the diploids set no seed, except when artificially pollinated by other individuals, and were presumed to be sexual and self-sterile (see chapter 9). The triploids set seed, with about 65-100% of the ovules setting good seed, the seed-set being roughly constant for each individual.

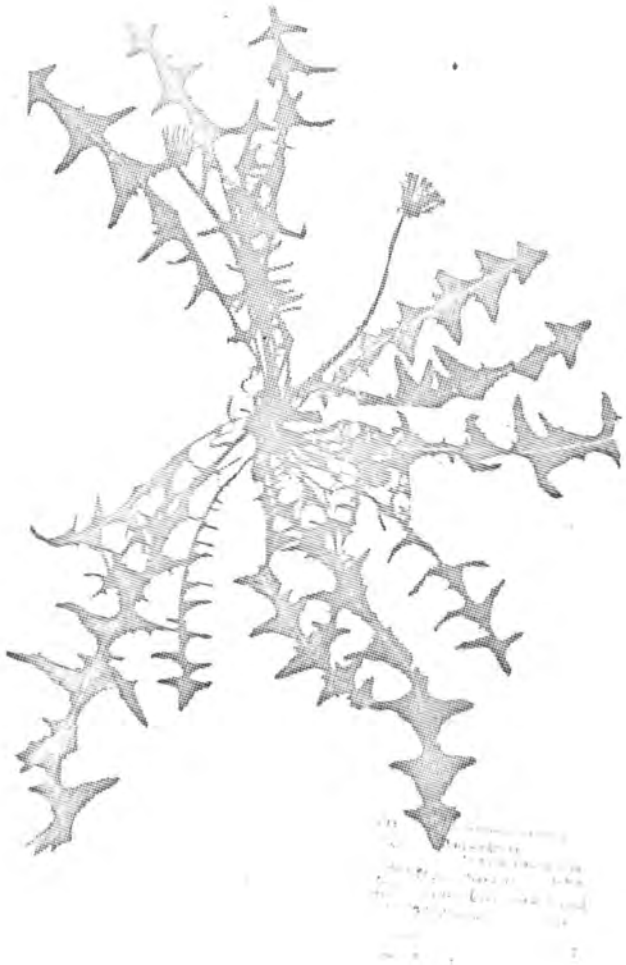


Photograph 23 Herbarium specimen of cultivated Tisophyllum; diploid sexual. From Kovacover Kopce, C.S.S.R.

x 1/4

Photograph 24. As for photograph 23, except that the plant was triploid and apomictic.

x 1/4



Photograph 25. Herbarium specimen of cultivated T. brachyglossum; a facultative triploid with reductional pollen. Greatham Creek, Co. Durham.

x 1/4.

The seed-set was of the same order when the heads were emasculated by slicing the florets off the head above the ovule about 3 days before anthesis, when the buds were about 10 mm high. This is the stage at which female meiosis occurs, and long before the precocious development of the embryo occurs in apomicts, to avoid the possibility of cleistogamous self-pollination having taken place. It seems well established that this triploid T.isophyllum was, unlike the diploid, behaving apomictically. It was of the greatest interest to me that the seed-set was usually far from perfect however. Most apomicts which I had grown in the same conditions set perfect seed whether emasculated or not. (These, in common with the triploid T.isophyllum showed near-perfect germination of all good seed, which can be very readily noticed by being coloured and full. Undeveloped seed is translucent, without any contents, and is extremely narrow. It seems unlikely that germination frequency is a characteristic of seed fertility in Taraxacum, but rather seed content.) The poor seed-set of triploid T.isophyllum is analysed in Tables 16 and 17. It will be noticed that some individuals of T.brachyglossum from Greatham Creek, Co. Durham, also showed bad seed-set of this type, and are included in the analysis. In all these plants, some families showed bad seed-set throughout, some showed bad seed-set in some individuals but not in others, while other families of the same species from the same localities showed good seed-set.

It seemed a possiblity that this bad seed-set might be a function of the meiotic behaviour of the female ovule, for it was immediately apparent that those plants with good seed-set had pollen of the restitutional type, while those plants with some bad seed-set had pollen of the

Seed-set in triploid Taraxaca from populations containing sexual Diploid Plants

Table 16. Progeny from different seed-heads in the same population. T.isophyllum v.S., Hlohovec C.S.S.R.

% Seed-set: in insect-proof greenhouse

65		100		100	
75		100		100	
75	mean	100		100	
80	78	100		100	
80		100	mean	100	
80		100	100	100	
90		100		100	mean
		100		100	100
		100		100	
		100		100	
		100		100	
				100	
				100	
				100	

Table 17. Progeny from the same triploid seed-head

% Seed-set: in heads from two siblings flowering in insect-proof greenhouse

85		40	
90		60	
90		60	
90		60	mean
90		65	61
95	mean	70	
95	94	70	
95			
100			
100			
100			

reductional type in the Greatham Creek population. All the T.isophyllum triploids showed had seed-set and reductional type pollen. It was clearly worth investigating the possibility that those plants with bad seed-set in fact had a partially reductional female meiosis, echoing the behaviour of the male meiosis reflected in the reductional pollen, and thus resulting in some reductional embryo-sacs which might be capable of sexual behaviour. This argument followed observation of the fate of the male meiosis of these plants, in which some meiotic nuclei were rather regular, bivalents chiefly being formed, and which segregated into rather regular tetrads; and other nuclei in which a higher number of irregular associations, chiefly univalents, were found, in which partial or complete restitution was occurring (q.v.). Why should this not be also happening in the female meioses of these plants, leading to facultative sexuality in the triploids, and thus accounting for the conspecific diploids found in one of the populations, at Kovacover Kopce?

An obvious initial test was to artificially pollinate the heads of these triploids with bad seed-set, to see if the seed-set was thus improved by fertilising the presumed sexual ovules which were not setting seed in the insect-proof conditions. A number of these flowers were pollinated artificially with diploid T.isophyllum (using the technique of rubbing the flower-heads together, see chapter 9) and the seed-set of all these plants showing bad seed-set improved markedly after pollination (see table 18).

Another test to see whether facultative sexuality was in fact occurring was also performed. It was argued that if certain ovules

Table 18. The effect of pollination by diploid plants on triploid T.brachyglossum Dt. from Durham, England, showing bad seed-set in insect-proof conditions

% seed-set	Unpollinated	Pollinated
164D	35	80
	35	80
	40	100
	45	100
	55	100
	60	
	60	
	65	
	85	
171C	65	70
	65	70
	85	
	95	
	100	
163A	70	85
	80	90
	85	95
	95	100
Means	69.5	90.0

contained reductional embryo-sacs, capable of behaving in a sexual manner, that when pollinated with haploid pollen from a sexual diploid, the seed arising from the reductional ovules would be expected to be diploid, and the progeny thus partially sexual in behaviour. In view of the fact that pollen regularity seemed a good indicator of the diploid state, it was decided to plant out numbers of progeny of the cross triploid T.isophyllum ♀ x diploid T.isophyllum, and triploid T.brachyglossum ♀ x diploid T.isophyllum, together with controls of non-pollinated seed from plants with bad seed-set, and pollinated seed from plants of T.brachyglossum showing perfect seed-set. The results of the examination of the pollen of all these progeny are tabulated in table 19. It will be noticed that the only offspring to show some plants with regular pollen are those resulting from plants with bad seed-set, pollinated. None of the controls contained any putative diploids. This result strongly suggested that reduction and sexual behaviour was only occurring in the ovules of the triploids of both species that were giving rise to bad seed-set. In order to confirm that sexual diploids were indeed arising from the triploids plants were repotted from 2 families which had shown some individuals with regular pollen (one family from each species involved were used). It was unfortunately impossible to know which of the individual plants from each of the two families had shown regular pollen, as the heads collected for pollen examination did not come from individually labelled plants. Nevertheless, of the 12 plants repotted, 6 from each family known to contain plants with regular pollen, two were diploid 2n=16, and two were hyperdiploid 2n=18 and 2n=c.20, and all four showed totally sexual

Table 19. Results of the examination of the progeny of triploid apomictic plants with bad seed-set, pollinated by diploid plants in insect-proof conditions

Cross	Sample size	Pollen regular	Pollen irregular	% regular
164 x 148	13	9	4	69.
158 x 148	9	6	3	66.
173 x 148	30	10	20	33.
171 x 185	24	4	20	16.7
164 x 154	14	3	11	21.4
	90	32	58	35.5%
Controls				
173 unpollin.	28	0	28	0
156 x 185	14	0	14	0
177 x 185	22	0	22	0
404 x 183	19	0	19	0
164 unpollin.	31	0	31	0
164 x 147c (autopolyp.)	10	0	10	0
	124	0	124	0

characteristics, setting no seed in insect-proof conditions, except when cross-pollinated.

It was now proven that sexual diploid plants could arise from triploid Taraxaca showing at least some agamospermy. It was still not clear what was the exact method by which this could occur however. As I have already stated, it was suspected that this was due to an irregular female meiosis, with synapsis, and partial or complete reduction in some cells, but also with the majority of meioses sufficiently irregular to inhibit segregation at 1st anaphase, resulting in some restitution. It was thought that embryological studies of triploids with bad seed-set might provide a lead in this direction. As is related in chapter 5, it was found that triploids with bad seed-set showed a proportion of undeveloped embryo-sacs, 12 hours before anthesis, together with well developed embryos in the same head. Undeveloped embryo-sacs in obligate apomicts have always withered by this stage, and the embryo-sacs in these triploids were indistinguishable from a sexual Taraxacum embryo-sac.. Two stages of female meiosis were found, and in each it is quite apparent that a synaptic meiosis is proceeding. In one preparation segregation can be seen to have occurred. This is the first evidence of a reductional female meiosis in a polyploid Taraxacum.

In view of the fact that some triploid Taraxaca can be shown to be the progenitors of diploid sexuals, it is clearly of great interest to gain confirmation of Fürnkranz's findings that diploid sexuals pollinated with pollen from tetraploid T.palustre, give mostly triploid progeny, which are only 25% apomictic. He also finds that interspecific (± = inter-

sectional) hybrids between diploids show a strong tendency to become polyploid through somatic mutation.

In my experience (which admittedly does not cover many Palustria) no naturally occurring tetraploids ever have much tetrad (n=16) pollen, and that which does occur is mostly rather irregular. Assuming that 'T. palustre' produces mostly tetrad pollen, it is surprising that such a high degree of sexuality prevails in the triploid hybrids. Fürnkranz has not, to my knowledge, ever pollinated a diploid with pollen from a polyploid of the same species, and it is in the result of this experiment that we are bound to be interested if we are to determine whether a sexual/apomictic polymorphism occurs in the field. I pollinated a number of heads of diploid T.isophyllum with pollen from triploid T.isophyllum. The chromosome numbers of the resulting progeny are shown in table 20. If a comparison is made with chromosome numbers in the wild population (table 15), it will be noticed that the two tables show a great discrepancy in the interploid chromosome numbers. Whereas the artificial crosses show a peak at 2n=18, and continue right through to 2n=24, the naturally occurring plants are mostly euploid. It is thought that this may be due firstly to the fact that all the artificial crosses are a result of pollination with irregular pollen from a triploid, while many of the naturally occurring plants will be a result of diploid x diploid, or triploid agamospermic parentage, thus keeping the same chromosome number as the parent(s). Far fewer interploid plants would therefore be expected to arise in the field. Secondly, I have yet to grow to maturity a plant with a chromosome number between 2n=19 and 21 inclusive.

I believe these plants must be weak or inviable (the counts recorded come from seedlings before establishment). In both the wild and artificial populations, plants from 2n=16-18 proved to be entirely sexual (and fully fertile), and those from 2n=22 to 24 mostly agamospermic, although the 3 plants in this range created by a diploid x triploid cross shared with the wild triploids a seed-set of approximately 70% without pollination and were presumably facultatively apomictic.

Table 20. Chromosome numbers of the progeny of a diploid female x triploid cross. T.Isophyllum Hagl.

2n=	16	17	18	19	20	21	22	23	24
	3	6	14	3	2	2	0	1	2

Before discussing the mechanisms of sexuality and apomixis more fully, it is worthwhile considering the male and female meioses of Taraxacum in greater detail. It has already been noted that the pollen of Taraxacum can be shown to originate from a restitutional meiosis, an irregular reductional meiosis, or a regular reductional meiosis, and that these different meiotic types are rather closely correlated with the chromosome number of the plant. These different meiotic types are pictured in photographs 26-32, and the meiotic and tetrad analyses of reductional and restitutional triploids are tabulated in tables 21-24. It is apparent that sexuals are only found in conjunction with plants with irregular reductional pollen, and that these latter are exclusively triploid. This conclusion became very clear during the analyses of the pollen of

Table 21. Meiotic analysis, T.hamatum Raunk., County Durham

I	II	III	Total	
	6	4	24	
4	4	4	24	
	3	6	24	
2	2	6	24	
	3	6	24	
	3	6	24	
		8	24	Strong association type meiosis
2	2	6	24	
3	3	5	24	
2	2	6	24	
2	2	6	24	
1	4	5	24	
1	4	5	24	
		8	24	
	6	4	24	
	3	6	24	
	3	6	24	
Mean 1	2.9	5.0		

Table 22. Meiotic analysis, T.praestans Dt. County Durham

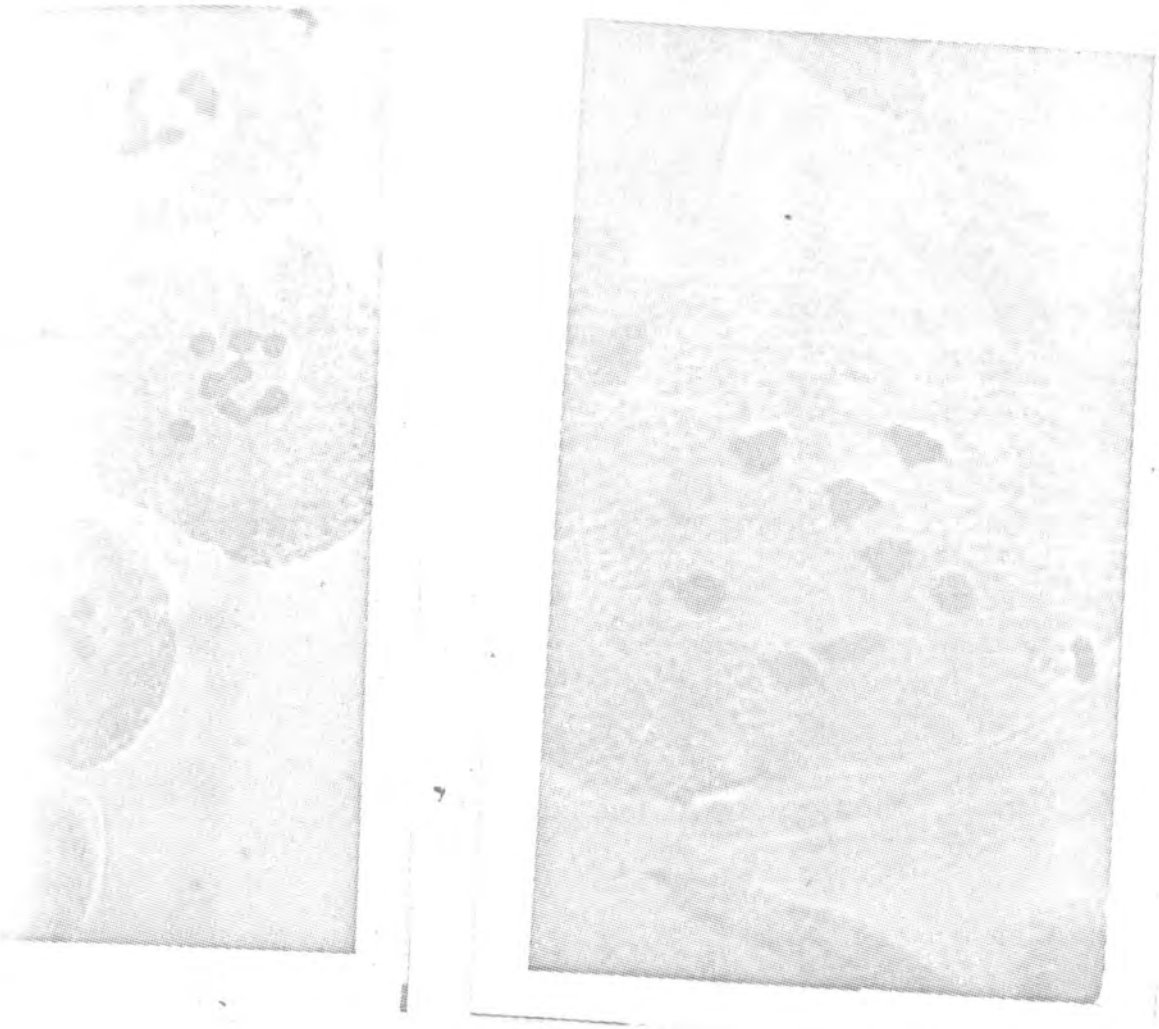
I	II	III	Total	
19	1	1	24	
22	1		24	
24			24	Weak association type meiosis
20	2		24	
24			24	
11	5	1	24	
18	3		24	
Mean 15.8	1.7	0.25		

Table 23. Tetrad analysis in Triploid T.hamatum Raunk. From County Durham. High tetrad type resulting from strong association type meiosis

Monad	Dyad	Triad	Tetrad	Pentad	Hexad
	14	7	27	5	2
	1	26	58		
	8	34	33		
	4	11	46	7	3
Total	27	78	164	12	5
Mean %	9.4	27.2	57.5	4.2	1.7

Table 24. Tetrad analysis in tetraploid T.naevosum Dt. from County Durham. High dyad type resulting from weak association type meiosis

	Monad	Dyad	Triad	Tetrad	Pentad	Hexad
TOTAL	7	107	28	119	5	1
Mean %	2.6	40.0	10.5	44.5	1.9	0.4



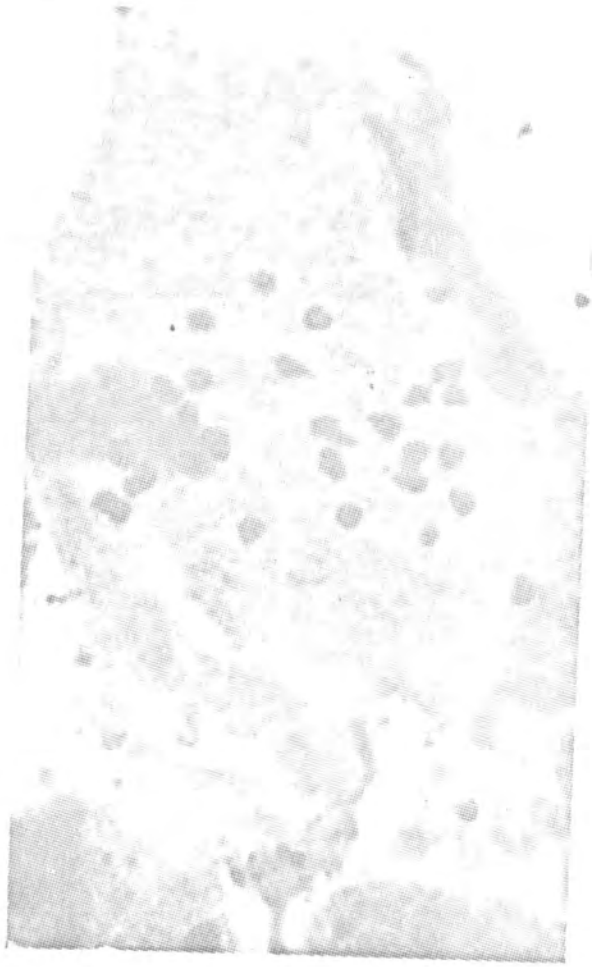
Photographs 26 and 27

Pollen mother cell squash preparation with Feulgen staining, showing diakenesis and metaphase I in diploid sexual T.bessarabicum, with 8 bivalents being constantly formed.

x 3000

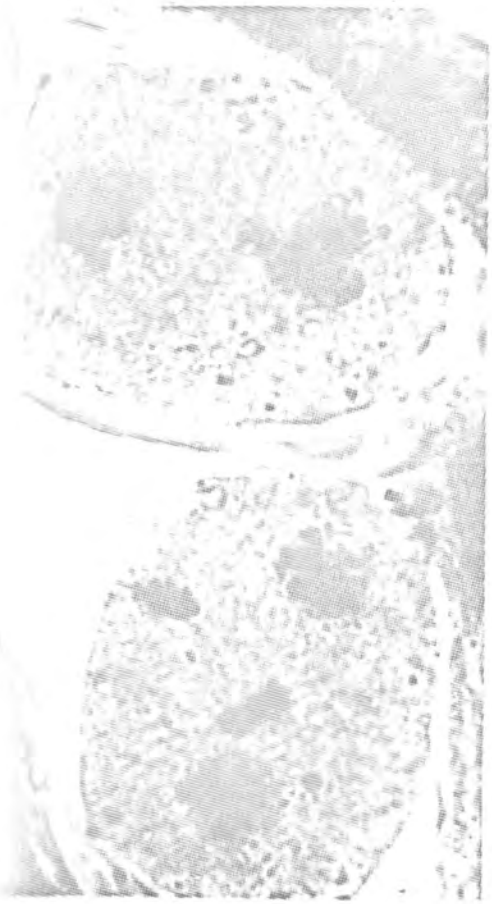
Photograph 28. Pollen mother cell squash with Feulgen staining, showing metaphase II in diploid sexual T.bessarabicum, n=8

x 2000



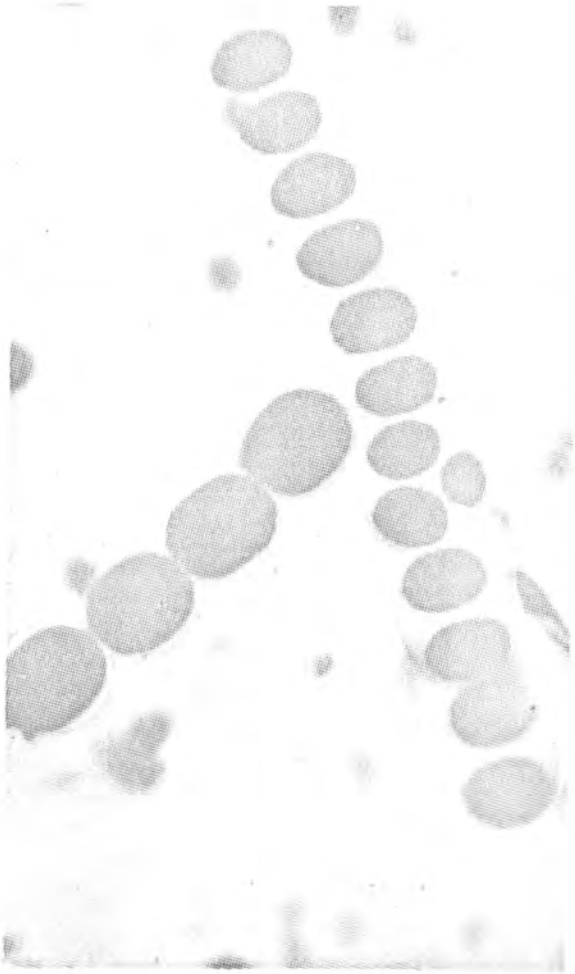
Photograph 29. Pollen mother cell squash with mordanted aceto-carmine staining showing metaphase I in an asynaptic meiosis, n=24, T.naevosum.

x 3000



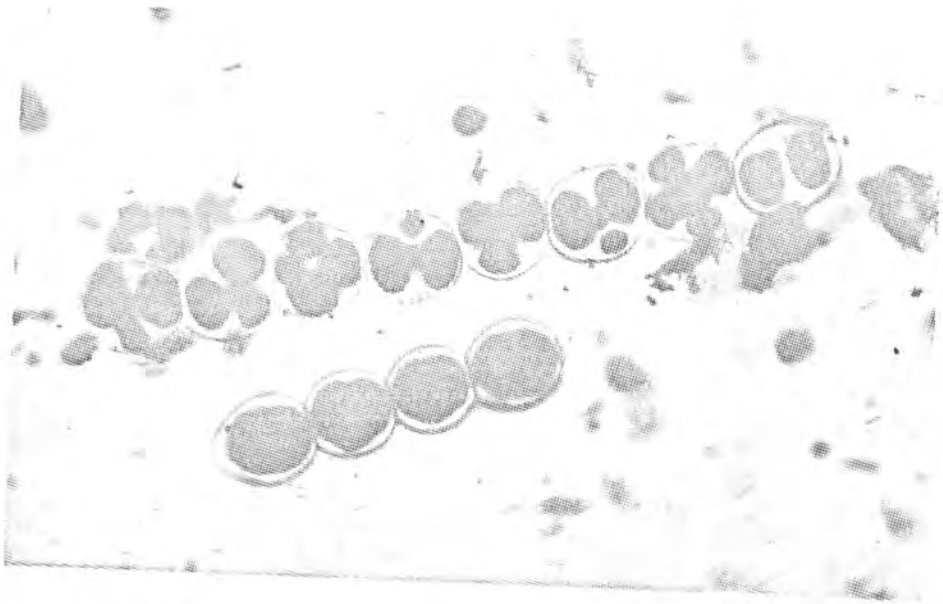
Photograph 30. Pollen mother cell squash preparation with mordanted acetocarmine staining showing wholly and partially restitutional telophase II in T.naevosum.

x 1200



Photograph 31. Pollen mother cell squash preparation with mordanted acetocarmine staining showing diads and triads in T.naevosum.

x 600



Photograph 32. Pollen mother cell squash preparation, with mordanted acetocarmine staining showing irregular reductional tetrad formation in triploid, facultatively apomictic T. subcyanolepis.

x 400

British populations, as regular pollen was unfailingly found in populations which otherwise possessed pollen which was irregular, but in the main reductional. As sexual plants will have a reductional female meiosis, I wondered whether the female meiosis of triploids with reductional pollen might not also be in part reductional. If this was the case, that the female meiosis, in some plants at least, echoed the male meiotic behaviour, some female gametes would be reductional and others restitutional in the same flowering head. As an egg-cell which is to develop apomictically normally requires to be restitutional, and as a sexual egg-cell is reductional, this seemed an interesting point to follow up, in the investigation of the facultative apomicts. As is related earlier in this chapter, and also in chapter 5, a reductional and synaptic female meiosis has been found in a triploid with bad seed-set, and reductional pollen. We are still a long distance from proving that in some triploids the female meiosis shows a similar behaviour to the male, which is unfortunate, as the male meiosis is a great deal more easy to examine that the female. Nevertheless, it now seems likely that the female meiosis is important in determining the reproductive behaviour of an ovule. Only a great deal of work on the female meiosis can prove that this is correct, and I am expecting to engage upon this project next. Unfortunately, the most complete analysis of the female meiosis in Taraxacum by Gustafsson (1933, 1934a,b) does not lead us to believe that this view is correct. In Gustafsson's three main research organisms, T.dissimile, T.kalbfussi, and T.norstedtii there was no indication that the male and female meioses were essentially similar. The first species does not have pollen, but

displays an asynaptic female meiosis (with secondary associations). T.kalbfussi has a rather asynaptic, but very irregular male meiosis, of the type that might produce 60% diads (as in T.oxoniense, for instance). The female meiosis however is once more devoid of primary associations. In T.norstedtii, which is a hexaploid, unlike the other two, which are triploids, the male meiosis is rather regular, with mostly bivalents formed, and although segregation is rather irregular, the pollen is almost entirely reductional. The female meiosis once again is asynaptic and restitutional however. (T.norstedtii is an exception amongst higher polyploids in that it retains the ability to form pollen at all). If we examine these results, it becomes clear that only T.kalbfussi is relevant to our problem. Higher polyploids have never been suspect of any type of sexuality, and T.norstedtii is the only species I know of above the triploid level which produces reductional pollen. It has been suggested that T.norstedtii is an autoploid, and I have recently found a closely related tetraploid which I have called T.pseudonorstedtii. There might therefore be a very high homology between a number of sets of chromosomes, which results in a higher degree of pairing at male meiosis than one might expect. In T.dissimile there is no male meiosis. In T.kalbfussi there is clearly a strong difference between male and female meiosis. There is no reason however why some species should not have attained a totally asynaptic female meiosis, while retaining some synapsis in the male meiosis, while other species maintain the same behaviour in both types of meiosis. T.kalbfussi is of the same type as a number of triploids and tetraploids with rather asynaptic male meioses, with some restitution,

and yet in these plants there is no suggestion of sexuality. Clearly we have to propose that the evolution of asynapsis in species occurred preferentially on the female side. This suggests that some kind of external system in the ovule creates the mutual repulsion in early asynaptic female meiosis recorded by Gustafsson. Gustafsson has supposed that this might be an enzyme system. It seems possible that the facultative apomicts, the high association plants, may be species in which this asynaptic system, also shown to a lesser extent in the male meiosis, has not evolved.

Before we finally examine our information relating to the causes and mechanisms of agamospermy, it is worth adding one further piece of evidence. This is of a rather different nature; it concerns the nature and reproductive behaviour of autoploids. The connection between diploidy and sexuality has already been fully emphasised. The question arose in our mind as to whether the diploid state did not allow agamospermy, by virtue of its chromosome content or meiotic behaviour, or whether all the diploid sexual species possessed some genetic information which was not present in polyploids, or which was obscured in the polyploid. One way of obtaining information on this subject seemd to be by making a diploid polyploid, without recourse to pollination by polyploid apomicts, through the technique of colchicine-induced polyploidy. The technique which was used in these experiments is described in appendix 1.

Seedlings from a number of diploid species were treated with colchicine. When the seedlings had reached the age of two months, epidermal strips were peeled from the top surface of the leaf(a very simple operation in this genus) and the diameter of 10 stomata measured for each leaf (to be

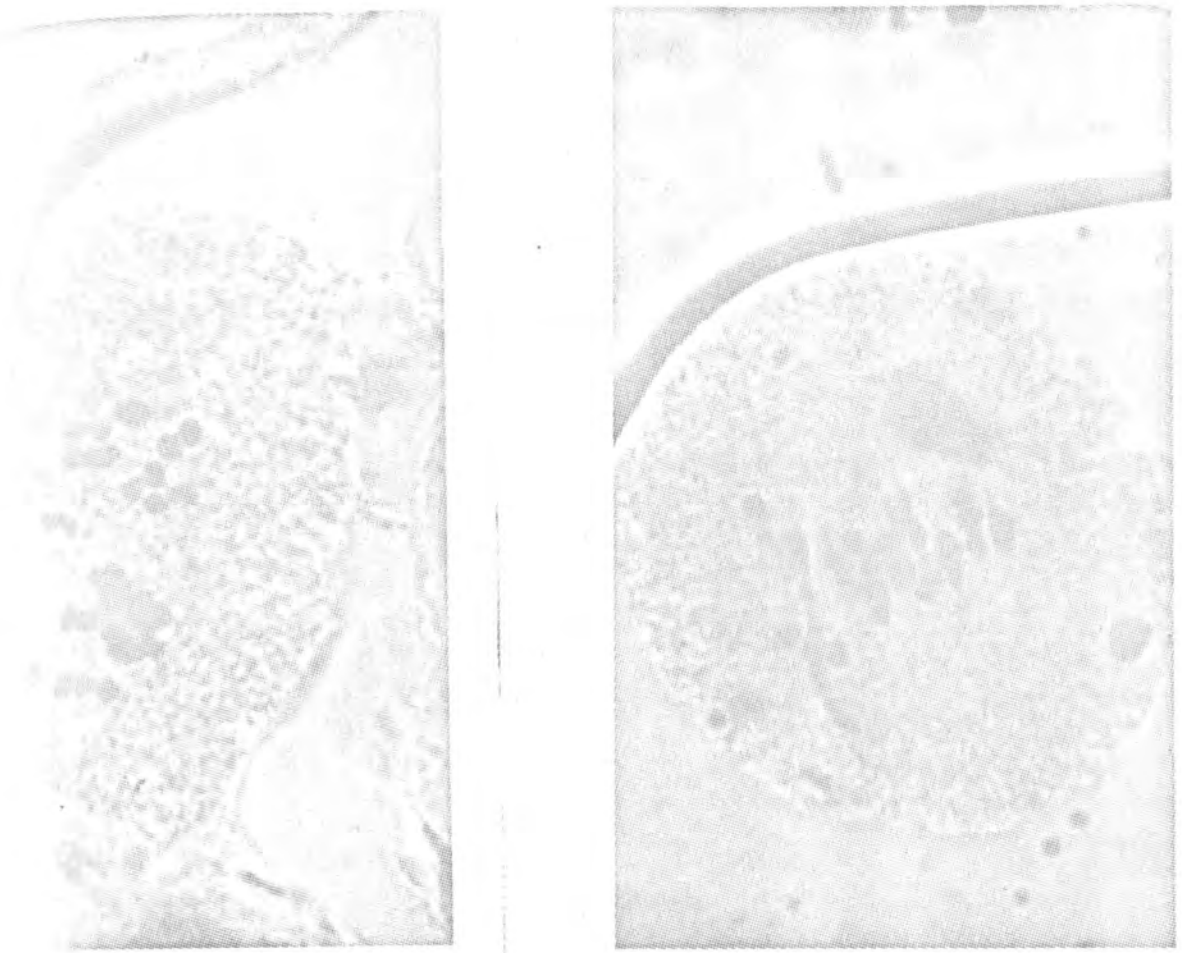
entirely accurate, the greatest distance at right angles to the line of the guard cells, from the outer wall of one guard cell to the outer wall of the other was measured after the tissue had been immersed in tap-water for ten minutes; by this time the stomata were invariably fully opened). It was found that untreated plants possessed stomata with a diameter of between 8 and 9 units (I did not calibrate the eye-piece micrometer gauge) while treated plants showed stomatal diameters of either 8-9 units, or 11-14 units. The two types were very clearly demarcated, and it was assumed that the plants with the larger stomata had become polyploid. A number of these died, and most of the remainder did not flower. In T.viride, the plants with large stomatal size were all stunted, with thick mishapen leaves, and none have flowered, although the plants with small stomata which survived are of normal morphology, and have flowered freely. In no other species was there any other external sign of presumed polyploidy. In T.serotinum, none of the treated plants have yet flowered, as this plant never flower until its second autumn. In T.isophyllum, two plants with large stomata have flowered, and it is with these that we are concerned. The species treated with colchicine and their subsequent fates are recorded in table 25.

Table 25. The results of colchicine treatment on diploid Taraxacum seedlings

Species	percentage with large stomata	percentage with large stomata surviving	Number flowering	Chm. No.	Sexual ?
T.isophyllum	43	25	2	32	Yes
T.viride	73	70	0	-	-
T.serotinum	15	100	0	-	-
T.bessarabicum	0	-	-	-	-
T.kotschyii	0	-	-	-	-
T.isophyllum x	0	-	-	-	-
T.polyodon	0	-	-	-	-

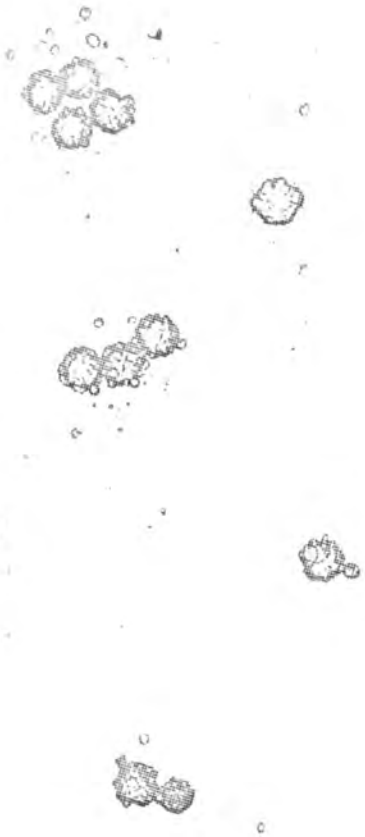
The last cross was colchicined in the hope that a hybrid might exhibit behaviour at variance with that of the tetraploids arising from single species. Unfortunately, none of the seedlings became polyploid, and this experiment will have to be repeated.

As can be seen, the colchicining experiments were only successful with regard to T.isophyllum. These two plants were both shown to be entirely tetraploid (photographs 32, 33), and possessed regular pollen of the same size as the diploids (photograph 34), despite the fact that they were n=16, not n=8. These plants flowered freely, and were totally sexual and self-sterile. Crosses were made between the tetraploids and diploid T.isophyllum. Good seed was set in the crosses in both directions, and the F1 has thrived in both cases. In both crosses, the F1 is entirely triploid (photograph 35). Here the resemblance ends however. Although both



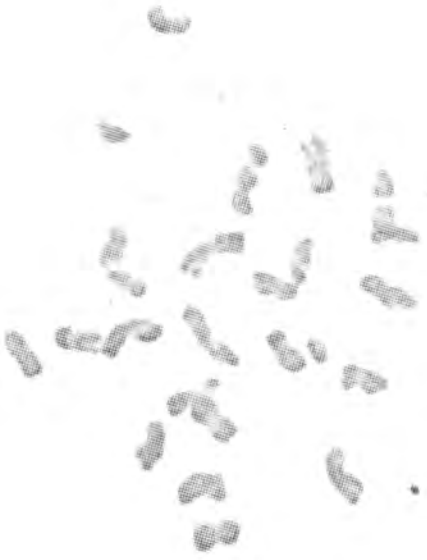
Photographs 33 and 34. Pollen mother cell squash preparation with Feulgen staining of meiosis in a colchicine-induced tetraploid T.isophyllum, n=16. Note regular pairing. This plant remained sexual, despite its polyploid condition.

x 3000



Photograph 35. Regular reductional pollen of triploid backcross from colchicine-induced tetraploid T.isophyllum.

x 800



Photograph 36. Root-tip squash preparation with Feulgen staining of T.isophyllum. These triploids were sexual or sterile, depending on the direction of the cross.

x 3000

families showed good regular pollen, like both parents, the 2n=32 female x 2n=16 male triploid proved to be totally sterile, while the 2n=16 female x 2n=32 male was as fertile as either parent. No agamospermy could be detected in any of these plants, despite repeated emasculations. Thus whereas the diploid and tetraploid plants were fully fertile, and the pollen of the triploid is also apparently fertile, the triploid ovules are incapable of functioning in any manner in plants resulting from tetraploid mothers.

It has been suggested earlier in this chapter that the key to the reproductive behaviour of a Taraxacum plant may be the fate of the female meiosis, but that agamospermy is unable to function without an additional and uncorrelated precocious embryogeny, which cannot develop with a haploid egg-cell. The autotetraploid was entirely sexual, and from the chromosome number of the off-spring when crossed to a diploid, we can assume that it had a fully reductional female meiosis resulting in a n=16 egg-cell. From this information we may surmise that the female meiosis was regular, with very few if any univalents or multivalents forming. On the other hand, the triploid was sterile in plants with a maternal tetraploid. As all the genomes present in all these plants would be identical, these facts are at present inexplicable. We can only assume that in one family the meiosis of the autotriploid was sufficiently regular to allow good segregation to reductional megaspores, while in the other, the meiosis was irregular, so that no reduction was possible. In this case, we note that the plant was not agamospermic, so that the mechanism ensuring the development of the ? restitutional egg-cell could

not have been present. And yet, this plant comes from a population in which triploid facultative apomicts of the same species in an apparently polymorphic relationship with the sexuals. Clearly triploidy is not by itself enough to initiate agamospermy, and when a triploid pollinates diploid sexual in these populations with some triploid apomictic offspring resulting, the triploid pollen apparently contributes a genetic system which allows the triploid unreduced egg-cell to develop precociously.

If a diploid was homozygous for a gene which automatically produced precocious embryos, the offspring would be haploid, and thus presumably at a considerable disadvantage (always supposing that the meiosis of diploids is always reductional , which seems to the the case). There seems to be no alternative but to suggest a genetic system controlling precocious embryogeny, which only works in the presence of unreduced egg-cells. This seems quite a plausible theory, particularly as haploid embryos may abort at a very early stage in their development. If we suppose this to be so, diploids would be sexual, whatever their genetic constitution. Triploids would be apomictic, if theypossessed the gene system for precocious embryogeny, and unreduced egg-cells. Reduced egg-cells would of course be sexual. If unreduced egg-cells occurred in a plant without the genetic equipment for precocious embryogeny, they would presumably cease to function.

The only difficulty with this theory seems to be that the selection pressure in populations containing some apomicts for precocious embryogeny would be intense (plants not possessing this system being sterile), and yet

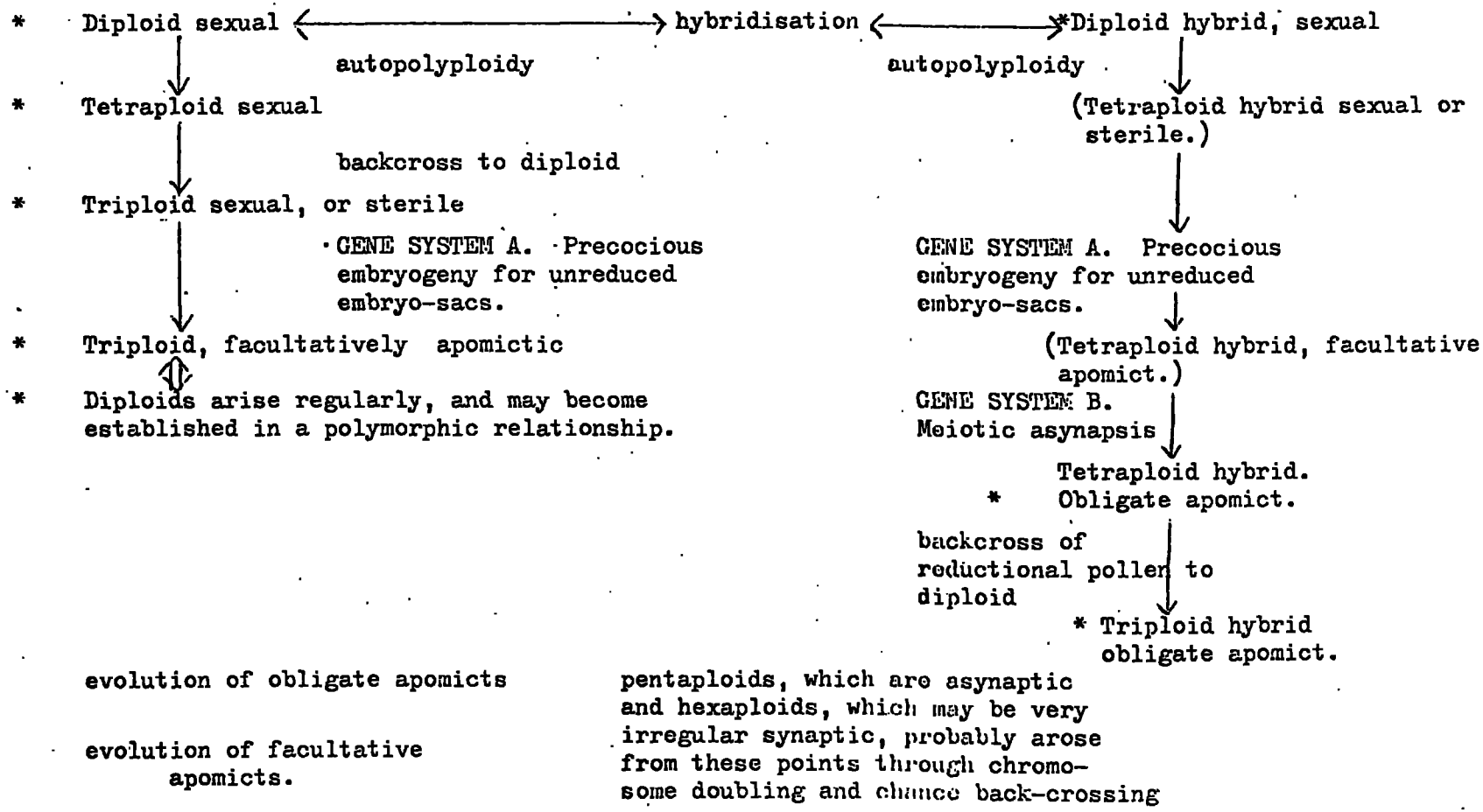
our artificial triploid is apparently of this type, without a precocious embryogeny system. There is a pressing need for the repetition of this experiment, which appears to be unreliable, not only from its distressing inability to fit in with the rest of my data, but also from the widely different results obtained from apparently identical plants. We can only suppose that the sterile plant from the maternal tetraploid was an unusual mutant form, in the absence of other data. The other artificial triploid, which was sexual, we can suppose had rather good meiotic pairing, perhaps as a result of its autoploid origin (see my earlier comments on T. norstedtii).

A scheme which represents my theories concerning the origin of apomixis in Taraxacum is set out in diagram 11. This is a condensation of many of the views expressed in this chapter. It makes the important additional point that some triploids may have evolved from backcrosses of tetraploids to diploids before an asynaptic restitutional meiosis evolved in the tetraploids. This scheme may explain why both reductional and restitutional types seem to occur in the triploids, but only restitutional meioses are found in tetraploids. It suggests that the potential for precocious embryogeny arose before that for restitutional meiosis, so that triploids, with an irregular meiosis, may have been among the progeny of wholly or mostly sexual tetraploids. When these tetraploids later developed an asynaptic restitutional meiosis, they may also have backcrossed to diploids resulting in mostly restitutional triploids.

This scheme follows the facts as we know them, but it extends beyond knowledge into the realms of speculation. It presents merely what I

consider to be the most likely way that apomixis may have evolved in its various types in this genus.

Diagram 11. A possible scheme for the evolution of apomixis in Taraxacum



* I have grown plants of this nature.
( ) I have not yet found Taraxaca showing this behaviour

Diagram 15. The known distribution of sexual Taraxaca in western Eurasia.

Chapter 9

HYBRIDISATION

Very little hybridisation has been observed in Taraxacum, and very few artificial crosses have been attempted in cultivation. This is doubtless due to the relatively recent discovery of sexual plants in this genus, and the difficulty found in obtaining most of them. The first attempts at interspecific hybridisation were made by Poddubnaja-Arnoldi (1939). She made all possible crosses between the sexual species T.kok-saghyz, T.multiscaposum, T. bessarabicum and T.serotinum, and she also crossed the pollen of the apomictic species T.hybernum, T.brevicorniculatum and T.'officinale' onto all of these sexuals. She found that T.kok-saghyz and T.multiscaposum set good seed when pollinated by the sexual species, but no seed when pollinated by the apomicts. As two of the apomictic species are tetraploids, and thus can be expected to produce restitutional pollen which will not function on the stigmas of sexual species, probably through a mechanical effect of size, this is not surprising. T.officinale might have been anything, including a tetraploid. Results from this work which are rather more curious are those regarding the other two sexual species, T.serotinum and T.bessarabicum. These did not set any seed when pollinated with any other sexual species. Yet these two species are usually (always?) self-fertile, and good seed would be expected to set, irrespective of the crossability of the species in question. All the hybrids that Poddubnaja-Arnoldi was able to create set very bad seed, and were mostly totally sterile. This result does not agree with the general conclusions of my

work, but I have yet to make any of her crosses except T.serotinum x T.bessarabicum and, as I would expect between these two self-fertile species, seed-set was very good. I have not yet germinated the seeds from this cross to discover whether hybridisation has occurred.

The only other worker to report the results of experimental hybridisation in Taraxacum has been Fürnkranz (1960, 1961, 1965). He reports both the discovery of hybrids in the field, and the synthesis of hybrids in the experimental garden. He found that all the taxa with which he was working were interfertile, and that crosses could be successfully performed with a triploid apomictic male parent. Where the results of these crosses are of interest in the present work, they are discussed in chapter 8. Fürnkranz reports the discovery of hybrids swarms between T.officinale and T.laevigatum (the Vulgaria and the Erythrosperma?), a situation that I have found in England. It is unfortunate that the old aggregate names of Handel-Mazzetti should have been used in this interesting work. The names T.officinale, T.laevigatum, T.palustre, T.alpinum and T.obliquum are virtually without taxonomic meaning, being in most cases the result of very heterogeneous typification, and in most cases not even being equal to a section. Even in this ancient classification, we must be uncertain about the taxonomy. Not only have no vouchers been deposited, or live material maintained, but the name T.obliquum is certainly incorrectly used. This plant occurs on the coasts of the Low countries, and has not been recorded within 800 miles of Vienna. It is probable that the brown fruited Erythrosperma (the Dissimilia Dt) are intended by this

epithet. From Fürnkranz's work we can adduce no more information than that he created hybrids between a number of different looking Dandelions, some of which were undoubtedly sexual, and that the hybrids possessed intermediate characteristics. In his latest paper (1966) he uses his results to destroy the biological foundation on which the justification of a microspecies classification lies (see chapter 1). It is difficult to see how Fürnkranz is able to condemn a system, particularly one which has stood the test of time and much usage, of which he patently has so little knowledge.

Nevertheless, there is much of value in Fürnkranz's work. He states that hybrids between diploid T.laevigatum and T.officinale showed triploid chimaeras, mitotic instability, and gave rise to triploid achenes in some cases. This is a most interesting lead to the type of origin that our polyploid apomicts may have had. These hybrids, he reports, closely resemble T.obiquum (the Dissimilia?) while hybrids between diploid T.palustre and T.laevigatum closely resemble T.officinale (the Vulgaria?) a very heterogeneous group! Nevertheless, the suggestion is made that many of our present day apomictic groups may be of hybrid origin, which must surely be correct. To suggest that hybridisation was a direct cause of apomixis, is going a little far perhaps. That hybrids might possess the necessary instability to give rise to polyploidy and unstable meioses seems to have been proven. It is significant that these triploids were sexual however (just as my autotriploids were). Clearly another factor is required to work upon a restitutional egg-cell-that of precocious embryogeny. Fürnkranz suggests that areas in which hybrids occur today possess more microspecies,

the inference being that these microspecies are apomictic segregates arising from hybridisation. In fact, if these segregates are successful, become well differentiated groups with geographic and ecological identity, there is no reason why they should not be given specific rank. Nevertheless, it is clear that this situation does not occur. In the hybrid populations which I know, a maximum of three species occur. It is true that a wide range of hybrid segregates some of which are apomictic, are found. But the variation is continuous, and the parental types are sufficiently frequent for their identity to be established, and the inference drawn that the hybrids are not very successful. A successful agamospermic strain, a candidate for specific rank, is unlikely to be fixed in an area where it is continually back-crossing with sexuals, unless it is genetically identical with the sexuals, as is clearly the case with T.isophyllum at Kavacover Kopce.

Furnkranz also notes that his plants were self-sterile. Małecka also reports self-sterility in the sexual T.pieninicum (1961) . Although both these observations escape remark, the question of self-sterility and self-fertility in apomictic Taraxaca is one of the greatest interest, which seems to have been ignored.

Information about the self-sterility/fertility of sexual Taraxaca can be summarised in table 26.

Table 26. Self-Sterility and Self-Fertility in Diploid Sexual Taraxaca

Section	Species	Self-fertile	Self-sterile	Reference
Leptocephala	T.bessarabicum	+		Personal
Serotina	T.serotinum	+		"
	T.haussknechtii	+		"
Rhodotrichia	T.kotschyi		+	"
Orientalia	T.stevenii		+	"
Macrocornuta	T.wallichii		+	"
Fontana	T.viride		+	"
Erythrosperma	T.austriacum		+	"
	T.isophyllum		+	"
	T.brachyglossum		+	"
Vulgaria	T.subcyanolepis		+	"
	T.polyodon		+	"
	T.duplidentifrons		+	"
T.'officinale'			+	Furnkranz 1960
T.'laevigatum'			+	"
T.'palustra'			+	"
T.'obliquum'			+	"

It will be noticed that whereas all the species belonging to otherwise agamospermic sections, and the two very primitive Asianspecies with very short rostra are self-sterile, the three primitive species with long rostra, found in the Mediterranean region and the Near-East, are self-fertile. It is difficult to envisage an evolutionary system whereby self-sterility could arise from self-fertility self-fertility always possessing the immediate advantage as long as cross-pollination is not complete (many authors inc. Stebbins 1950), and

one is thus forced to believe that the Serotina and Leptocephala are not on the main evolutionary line of sexual Taraxaca, but had evolved self-fertility, whereas the evolutionary development that we can suppose gave rise to the Western agamospermic sections did not evolve self-fertility. It is tempting to suppose that they did not need to, as agamospermy rapidly developed in these lines, and thus achieved automatic seed-set by another method. The remaining sexual lines in this evolutionary advance may also not have achieved self-sterility, although we unfortunately do not know the behaviour of T.obtusilobum, T.confertum, and T.pieninicum, nor do we know the behaviour of T.minimum and T.pyropappum, of the Mediterranean diploids, and of T.pumilum in that apparently quite separate advance of the Laevia. In fact of the totally sexual species in agamospermic sections, we only have information on T.viride, which is self-sterile. Of the 5 species and Fürnkranz's medley, which have been found in apparently polymorphic populations (see chapter 8), we know they are all self-sterile. As these plants belonged to populations which contained a seed-producing safety-factor in agamospermy, it is not surprising that self-fertility did not evolve. Crosses made to determine whether self-fertility is under simple genetic control, and whether it is dominant or recessive have so far failed to flower.

Sörensen and Guðjónsson (Sörensen 1958) have demonstrated a quite different kind of sexuality in Taraxacum (see chapter 8) in which certain monosomic triploids are capable of a limited sexuality. In several cases, diploid sexuals arose from a cross onto such a monosomic. Through these plants, and with the diploid sexual species T.obtusilobum these workers

carried out extensive hybridisation experiments inside the section Vulgaria, using 11 species all told. From certain monosomics pollinated by T.obtusilobum, offspring were obtained which were clearly of intermediate appearance between the two parents. These were either near-diploid, presumably caused by a reductional female meiosis, followed by fertilisation with haploid pollen, or about 2n=30, presumably through restitution followed by fertilisation by haploid pollen grain. Restitution seems to have occurred chiefly in the aberrant elegans (chromosome D missing, see chapter 7, 8); while ab.tenuis (chromosome H missing) shows mostly near-diploid offspring, presumably resulting from reduction. In both cases the genetic control of precocious embryo development seems to be missing, but with the loss of chromosome H, the loss of asynaptic control seems also to have occurred. In both cases the monosomics and the resulting diploid offspring produce fertile hybrids with all agamospermic plants; at a high rate in the diploid, which is entirely sexual; but the polyploids are usually agamospermic. In conclusion, it is safe to say that all reduced egg-cells in T.obtusilobum, the monosomic sexuals, or F.I. diploids, are capable of being fertilised by any pollen in these Vulgaria, and that the performance, breeding behaviour and seed-set, whether of sexual or apomicts, depends on the amount of chromosomal inbalance displayed in the meiosis, and on the chromosome complement of these plants. Plants of 2n=19, 20, 21, and probably some of 2n= 22 and 23 are uncertain in their performance. In my experience 2n = 19, 20 and 21 plants probably never germinate.

I have made a large number of crosses onto sexual plants belonging to 12 species. In the case of the three self-fertile sexual species, it is

only possible to say with certainty that hybridisation has occurred by examination of the offspring of the cross. None of the offspring from crosses onto T.serotinum, T.haussknechtii and T.bessarabicum are of a sufficient age for this to be determined. In all other cases the sexual species are entirely self-sterile, and it is therefore simple to determine whether hybrid seed has been set, in insect-free conditions. Unfortunately there have been occasions when the greenhouse has been invaded by insects after damage to the insect-proofing, or in very hot weather, when it has been necessary to leave the greenhouse door open for short periods. Throughout crossing experiments, I have left a percentage of sexual heads unpollinated as controls. In well over 90% of unpollinated heads (except of course in the self-fertile species) there has been no seed-set. In about 8% there have been 1-3 seeds set. In these very low seed-sets, cross-pollination is thought to have been by thrips or aphids, both of which have sometimes been present, despite regular fumigation with nicotine. In about 2% of the plants there has been a much higher seed-set, in the order of 20-40%, and in two instances as high as 60%. Larger insects such as Diptera, Apis and Bombus have occasionally been found in the insect-proof house, and it is thought that in these cases these are responsible. Nevertheless, it is clear from these controls that repeatable results for cross-fertilisation are likely to be reliable.

Pollination is effected by the simple process of rubbing the two heads together of plants just after anthesis, at a stage when the stigmas are loaded with pollen, but have not yet started to recoil back to achieve automatic self-pollination. It should be noted that the low figures of seed-

set for crosses in all intra and interspecific crosses (table 27) is due to the fact that not all the flowers on a Taraxacum head mature together. In the field, successive visits by insects make complete fertilisation a possibility. In the greenhouse, one cross is unlikely to fertilise more than 70% of the stigmas, even in optimal conditions. An average seed-set of 40% is usual in intraspecific crosses in table 27, and it will be noticed that the seed-set in many interspecific crosses in fact reach this level.

Although a large number of crosses have been made, the hybrid seed has been germinated and the breeding behaviour and fertility of the hybrid tested in only a few crosses. The results of these tests on the FIs are presented in table 29. In addition, the results of a large number of crosses onto facultatively apomictic triploids are presented in table 17. It is clear that some interspecific hybridisation occurred in this experiment, which was primarily designed for another purpose.

Table 27. Seed-set in inter-specific crosses

Female Parent (diploid)	Male Parent	No. of Crosses	Mean % of seed-set
T.stevenii	T.viride 2n=16	3	30
	T.polyodon 2n=16	1	0
	T.brachyglossum 2n=24	1	0
	T.stevenii	2	10
T.kotschyi	T.austriacum x T.fontanum 2n=18	1	20
	T.bessarabicum 2n=16		
	T.kotschyi		
T.wallichii	T.bessarabicum 2n=16	1	90
T.viride	T.stevenii 2n=16	2	70
	T.succulenteum 2n=32	1	15
	T.pycnostictum 2n=32[x]	1	10
	T.repletum 2n=32[x]	1	30
	T.fontanum 2n=24	1	10
	Tbrachyglossum 2n=24	3	13
	T.polyodon 2n=16	2	50
	T.polyodon 2n=24	1	25
	T.duplidentifrons 2n=16	2	30
	T.hamatum 2n=24	1	80
	T.austriacum x T.succulenteum 2n=17	1	8
	T.naevosum 2n=24	1	0
	T.austriacum 2n=16	1	0
	T.viride 2n=16	4	78
T.austriacum	T.succulenteum 2n=32	5	7
	T.naevosum 2n=24[x]	1	2
	T.fontanum 2n=24	2	50
	T.duplidentifrons 2n=16	3	47
	T.cimbricum	1	90

Table 27 (cont.)

Female Parent (diploid)	Male Parent	No. of Crosses	Mean % of seed-set
	T.brachyglossum 2n=24	14	24
	T.rubicundum 2n=24[x]	5	8
	T.isophyllum 2n=24	2	3
	T.isophyllum 2n=16	20	35
	T.austriacum 2n=16	23	42
T.isophyllum	T.kok-saghyz 2n=24	1	30
	T.euryphyllum 2n=32[x]	1	0
	T.fontanum 2n=24	1	60
	T.pycnostictum 2n=32[x]	1	0
	T.duplidentifrons 2n=16	1	0
	T.polyodon 2n=16	10	28
	T.disseminatum 2n=24	1	90
	T.rubicundum 2n=24	2	0
	T.brachyglossum 2n=24	21	35
	T.austriacum 2n=16	18	36
	T.isophyllum 2n=24	10	13
	T.isophyllum 2n=16	44	33
T.polyodon	T.stevenii 2n=16	1	25
	T.fontanum 2n=24	1	10
	T.viride 2n=16	2	51
	T.litorale 2n=24[x]	1	10
	T.brachyglossum 2n=24	1	50
	T.isophyllum 2n=16	8	37
	T.polyodon 2n=24	3	3
T.duplidentifrons	T.viride 2n=16	1	95
	T.austriacum 2n=16	1	10
	T.isophyllum 2n=16	2	36

x pollen chiefly diad.

Table 28. Total Seed-sets

	Type of cross	Sample size	Mean seed set, %
1.	Diploid sexual x diploid sexual, all species	150	34.6*
2.	Diploid sexual x triploid apomictic, all species	102	17.9*
3.	Diploid sexual x diploid sexual, same species	73	40.7
4.	Diploid sexual x triploid apomictic, same species	13	8.0
5.	Diploid sexual x diploid sexual, different species	123	37.0
6.	Diploid sexual x triploid apomictic, different species	74	24.0
7.	Diploid sexual x apomict producing mostly diad pollen (low association) marked with cross in table	14	7.0

All percentage differences in total seed-sets which show a significant separation are listed below: (significance at p=0.05).

1 with 2,7. The others are not relevant

2 with 1,7. "

7 with 1,2 "

3 with 4,6

4 with 3, 5, 6

5 with 4

6 with 4.

Table 29. Germination and performance of hybrids

Hybrid	% Germination	% Flowering (7 months)	Chromosome numbers	Sexual	Apomictic
T.viride 2n=16 x T.fontanum 2n=24	50	Nil	16, 17, 18		
T.viride 2n=16 x T.succulenteum 2n=32	70	2/9	18, 20	+	
T.viride 2n=16 x T.stevenii 2n=16	100	8/8	16	Seed-set 10%	
T.viride 2n=16 x T.polyodon 2n=24	50	1/9	17, 18	+	
T.viride 2n=16 x T.polyodon 2n=16	50	7/9	16	Seed-set normal	
T.viride 2n=16 x T.brachyglossum 2n=24	60	Nil	17, 18,20		
T.polyodon 2n=16 x T.isophyllum 2n=16	30	11/11	16	Seed-set 16-20%	
T.polyodon 2n=16 x T.litorale 2n=24	50	Nil	21, 23		
T.serotinum 2n=16 x T.bessarabicum 2n=16	70	Nil	16		
T.austriacum 2n=16 x T.fontanum 2n=24	80	4/6	17, 18, 19	Seed-set normal	2 (1 facul. 1 total)
T.austriacum 2n=16 x T.succulenteum 2n=32	100	17/17	16,18, 19	Seed-set normal	
T.austriacum 2n=16 x T.cimbricum (Apom.)	100	19/19	16, 18,21	Seed-set normal	1 facul.

It is clear that many more crosses between many more taxa are necessary before a definitive account of breeding barriers between sexual and between sexual and apomictic species in the genus can be given. Nevertheless, it is possible to draw several tentative conclusions from the data presented above in tables 27-29. The most obvious conclusion is that no absolute barriers to fertilisation seem to exist in those taxa that crosses have been made, and as these represent the full range of the evolutionary diversity found in the genus (except perhaps the Laevia), this may be true for the whole genus. An exception can be made for the numerous obligate agamospermic species which never bear pollen. There is no possibility that they can cross with any species at all. Seed-development and germination and development seem likewise to be unaffected by the cross. Where slight fertilisation barriers may exist (as in T.austriacum and T.viride when pollinated by the rather distant T.succulenteum in the Macrocornuta), these are not absolute by any means. Absolute, or very strong breeding barriers are only found when the pollen used is nearly totally diad. This diad pollen, which can germinate readily (witness the high polyploids found in Fürnkranz's and Sörensen's work) seems to be unable to pollinate many species. This is probably a mechanical failure due to the large size of the grain. It is too early to say that this may form an absolute barrier however, as in many cases it manifestly does not. As for the inability of T.stevenii to form hybrids with T.brachylobum and T.polyodon, only one pollination each was managed. T.viride, which formed fertile hybrids with T. stevenii is presumed to be equally advanced and rather related to the other species, so no conclusions can be drawn.

Chapter 10

CHARACTER INHERITANCE

In several of the sexual species cultivated, characters have varied in a clear-cut manner between individuals of a single family (siblings). As no intermediates have been detected in these cases, it is thought that these characters may be under the control of a single gene with a dominant allele, and that the families grown have either been the result of a heterozygote crossed onto a heterozygote (in which case the filial generation would be expected to segregate in an approximately 3.1 ratio) or a heterozygote back-crossed onto a recessive homozygote (with a resulting 1.1 ratio). As these characters may conceivably be of value in future experiments as marker genes, they are tabulated below (table 30).

Table 30

Species	Gene	Ratio	Dominant
T.serotinum (Jasi, Roumania)	Leaf entire E Leaf dissected e.	E 9 e 5	-? E
T.stevenii	Ligules striped red. L Ligules striped grey I	L 3 I2	-? L
T.isophyllum	Ligules striped dark puce p Ligules striped grey P	p 4 P 13	P
	Achenes purple A Achenes greyish a (f.achrycarpum)	A 9 a 4	-? A (confirmed below)
T.austriacum	Ligules striped dark puce p Ligules striped grey P	p 4 P 5	-?

So far only one cross has been made to verify some of the inferences drawn above. In this, a plant from a totally achrycarpous family of T.isophyllum was pollinated by a plant from a totally purple family of T.isophyllum (which may still have been heterozygous however). All the 11 offspring which have so far set seed are purple, thus confirming the dominance of A.

It is of interest to note that whereas the presence or absence of leaf dissection in T.serotinum and the achrycarpum mutant in Erythrosperma have been recognised in the literature as polymorphisms of no taxonomic importance, ligule stripes are of taxonomic importance in the Erythrosperma, and had not been recognised as being liable to intraspecific variation. In most species in this section they may of course be constant for a species, especially in the apomicts which have less opportunity for maintaining variation.

The achrycarpum phenotype has also appeared in 7 out of 9 offspring of a cross between sexual T.polyodon (Vulgaria, with brown achenes) and a purple T.isophyllum from an all purple family that we must presume was heterozygous. As the results of this cross agree with the presumptive parentage Aa (isophyllum) x aa, it seems that the Vulgaria, and indeed perhaps all non-red or purple -fruited species are homozygous for the allele.

Another interesting occurrence appeared in a cross between two families of T.isophyllum, in which 30% of the offspring were albino, without any green pigments. These naturally failed to establish. It would seem that both parents here were heterozygous for albinism, and that

¼ of the offspring were subsequently homozygous recessive, thus allowing the phenotype to appear. As the sample was rather large (approximately 50 seedlings) it is unlikely that the other possibility, that albinism is dominant, and a point mutation had occurred in the germ-cell initials of one of the parents, would derive such a close segregation to the expected 3.1 of a heterozygote cross.

In the few interspecific crosses which have been grown to flowering, it is not possible to trace the inheritance of all the characters, as we can suppose that most species would be homozygous for the important taxonomic characters, and thus the F1 hybrid would only show which characters are dominant. Where the hybrid possesses intermediate characters, it is not possible to determine whether this is due to incomplete dominance, or a polygenic effect. Where it has been possible to show that characters are dominant, or intermediate in the hybrids, these are tabulated below (table 31).

Notes on table 31

Key to the numbers.

1. 559. T.austriacum x T.fontanum
   560. T.isophyllum x T.polyodon
   563. T.isophyllum x T.succulenteum
   565. T.viride x T.succulenteum
   566. T.stevenii x T.viride
   569. T.viride x T.polyodon
   571. T.viride x T.polyodon
   572. T.austriacum x T.cimbricum

2. There was very little segregation of characters among the hybrids, suggesting that the species were mostly homozygous for the characters noted.

3. In 563 and 572 the offspring were very nearly entirely maternal in all characters. The interploid chromosome numbers of the offspring, and the high seed-set of the cross, together with the apomictic behaviour of two individuals of 572, suggest that the cross was effective, and that outside pollination from another T.austrianum individual was unlikely. It is possible that a rather complete pollination from triploid Erythrosperma occurred through a stray insect before I made the cross, or alternately, that most of the Erythrosperma characters are dominant. The other possibilities of spontaneous triploidy and apomixis and, or self-fertilisation seem

4. unlikely. In 559, 2 offspring were very weak, and of a maternal appearance, while another 3 were more robust, and intermediate in appearance. One of these was apomictic. Only the last three are definitely of hybrid origin and these only have been used in the table. The origin of the weak plants and of 563, and 572 should be solved by the results of a number of F2 crosses that have been made. If the plants are hybrid, characters should segregate in the F2.

5. All proven hybrids were very large, and most flowered rather sparingly. Some were of a very weak appearance and these are thought to be 2n=22 and 2n=23, having a triploid male parent. This has been proved in one case (2n=22). All had a very intermediate appearance, the character inheritance being as shown in the table. The gene inheritance is only known for the achrycarpum genotype, which is shown to control achene pigment in the Vulgaria as well as the Erythrosperma. Not all plants resulting from the crosses onto T.austriacum may be hybrid.

Table 31. Dominance of characters in F1 hybrids

Hybrid (for key see above)	Character	Complete dominance	? Incomplete dominance	? Poly-genic
560, 565, 566, 569, 571	Robust/slender	Much more robust than either parent		+ ?
560, 565, 566, 569, 571	Leaf length and breadth	Roughly twice as long as the longest parent		+ ?
565, 566	Leaf thick/thin	Thick		
566	Leaf bright green/dull green	Bright green		
560, 566, 565	Leaf glabrous/hairy	Glabrous		
565, 566	Leaf entire/lobate		+	+ ?
565	Leaf glaucous/green	Green		
560, 565, 566, 569, 571	Petiole purple/green		+	
560, 566, 571 559	Petiole winged/unwinged		+	+
560, 559	Leaf-lobes many, narrow/few, broad	Many, narrow		
566	Scapes glabrous/hairy	Glabrous		
566	Exterior bracts very marginate/not so	Very marginate		
560, 565, 559	Exterior bracts ovate/lanceolate		Tending to lanceolate	+ ?
560, 565, 566, 599	Exterior bracts erect/recurved	Recurved		
559, 560, 566	Exterior bracts corniculate/flat	Corniculate		
560	Flowers many/few		+	+ ?
559, 560	Ligules broad/narrow	Broad		
559, 560	Ligules striped grey/purple	Purple		

Table 31 (con.)

Hybrid	Character	Complete dominance	? Incomplete dominance	? Poly-genic
566	Achenes fusiform/ abruptly contracted	Fusiform		
566, 559, 560	Achenes with long narrow cone/conical	Long narrow cone		
566	Rostrum short, thick/ long, narrow		Rather long	

Chapter 11

HYBRIDISATION IN WILD POPULATIONS

The only recorded instances of Taraxaca hybridising in the field are given by Fürnkranz, and are discussed in chapter 9. He describes plants which he belives to be hybrid in nature, and using the microspecies terminology, these would in fact be intersectional hybrids. It is extremely unlikely that a taxonomist or an evolutionist would notice hybridisation in Taraxacum unless 1) he knew sexual plants from the area and 2) the parents were of different sections. In these circumstances, it is relatively easy to notice hybrids, even from herbarium specimens. I have recorded the following hybrids from herbarium material:

Table 12. Hybrids recorded from herbarium material

Female parent (sexual)	Male parent	Country of origin
T. serotinum	Vulgaria sp.	Roumania
"	Erythrosperma sp.	"
T.bessarabicum	Palustria sp.	Austria/Hungary
T.isophyllum	Vulgaria sp.	Czechoslovakia
Vulgaria sp.	T.anglicum	Britain
T.brachyglossum	T.polyodon?	"
T.subcyanolepis	T.oxoniense	"

I have not yet visited the population of Czechoslovakia and Austria in which sexual individuals seem to be so frequent, but according to Fürnkranz, hybrids are common, at least in Austria. As for Czechoslovakia, one of 12 seed heads brought from Kovacover Kopce showed both diploid and

triploid progeny from the same seed head, and thus must have been of a sexual ancestry of some kind (although whether from a diploid or triploid mother seems uncertain). These progeny were clearly T.isophyllum x Vulgaria sp. It can be expected that intersectional hybridisation may be frequent at localities where T.isophyllum occurs, always supposing a plentiful supply of Vulgaria-species, with which it seems perfectly interfertile.

In Britain, three species have been definitely shown to have sexuality, although others may, and probably do fall into this category. Of the three sexual species, it seems unlikely that T.austriacum is more than a casual (chapter 8). The other two, T.subcyanolepis and T.brachyglossum are both widespread species in grassland; the latter species at any rate being restricted to calcicole habitats. The former species belong to the Vulgaria, the latter to the Erythrosperma. The diploid T.subcyanolepis , not separable from the triploids of the same species, nevertheless contrives to appear unfortunately similar to the Scandinavian whollydiploid species T.obtusilobum. It is possible that it is indeed T.obtusilobum, and is specifically distinct from the triploid T.subcyanolepis which occurs with it; or that it closely resembles T.obtusilobum, but is in fact T.subcyanolepis in a diploid form, or that T.obtusilobum is in fact an aggregate name given to a number of diploid forms in Sweden, which may have belonged to one or more species including T.subcyanolepis and T.cyanolepis. I subscribe somewhat to the last possibility, and so these plants will be known as T.subcyanolepis in this country, T.obtusilobum being, although older, a nomen confusum.

Despite the fact that the diploids do not seem to be at a very high percentage in any of the populations investigated, considerable intersectional hybridisation seems to have occurred in some of the populations containing sexuals. The two sections Erythrosperma and Vulgaria are readily separated on a large number of characters, and this is even more true for the species T.subcyanolepis and T.brachyglossum. Although these species were probably providing most of the sexuals in the area, other species occurred in the areas investigated, and some of these doubtless acted as male parents. Furthermore, for the scatter diagram technique that I wanted to employ, characters with a continuous variability were requisite. Consequently, the following characters were used as the most representative of intersectional identity:

diameter of the scape, 1 cm. below the head, measured fully flattened;

diameter of the capitulum, when the florets stand, or are held horizontally;

length of the longest exterior bract which could be found that was not overlapped by another exterior bract, measured from the tip to the point of juncture with the scape, in the centre.

This data was collected from a minimum of 50 individuals from each of the 5 populations tabulated below in table 33. At the same time, heads were collected from each plant in order that the nature of the pollen of a plant with known characters might be determined. In addition, a minimum number of 50 seed samples were taken from each population, and a number of characters of intersectional importance listed for the seeds. The populations were chosen especially, as they were all suspected or known to contain sexual individuals. Sampling involved the subjective choice of an area, and

then walking in a straight line across it, picking a head from every flowering individual encountered.

Table 33. Populations sampled to investigate hybridisation in the field.

Sherburn Hill, Co. Durham. Short magnesian limestone grassland. This was dominated by Sesleria caerulea, although Taraxaca mostly occurred growing in sheep-tracks dominated by Festuca sp.

Species present: T.subcyanolepis (Vulgaria).

T.oxoniense (Erythrosperma).

Some T.lacistophyllum away from the main populations, growing on the quarry face probably does not participate in the hybridisation. It is a triploid with restitutional pollen.

Diploids, hyperdiploids andregular pollen have been found in T. subcyanolepis and hybrids at about 15% of total population sampled (perhaps at 20-30% in the species?).

Hybridisation considerable. At least half the plants have hybrid characters (see diagram 13)

Thrislington Plantation, Cornforth, Co. Durham. Habitat as above.

Species present: T.polyodon (Vulgaria).

(T.subcyanolepis Vulgaria)

T.oxoniense (Erythrosperma).

One plant with regular pollen was a hybrid, but it was not thought that T.polyodon, the chief Vulgaria-species present, which, like T.oxoniense only has slightly reductional pollen, was a parent. The Vulgaria parent might have been T.subcyanolepis. No cytology. Hybridisation slight. Perhaps 10% of the plants have hybrid characters.

Diagrams 11 and 12

Scatter diagrams of populations containing representatives of the Vulgaria and Erythrosperma, in one of which (Seaton Carew on the left) sexual plants have not been found, and in the other (Sherburn Hill, on the right), sexual individuals occur. See chapter 9 for further information.

Diagram 11

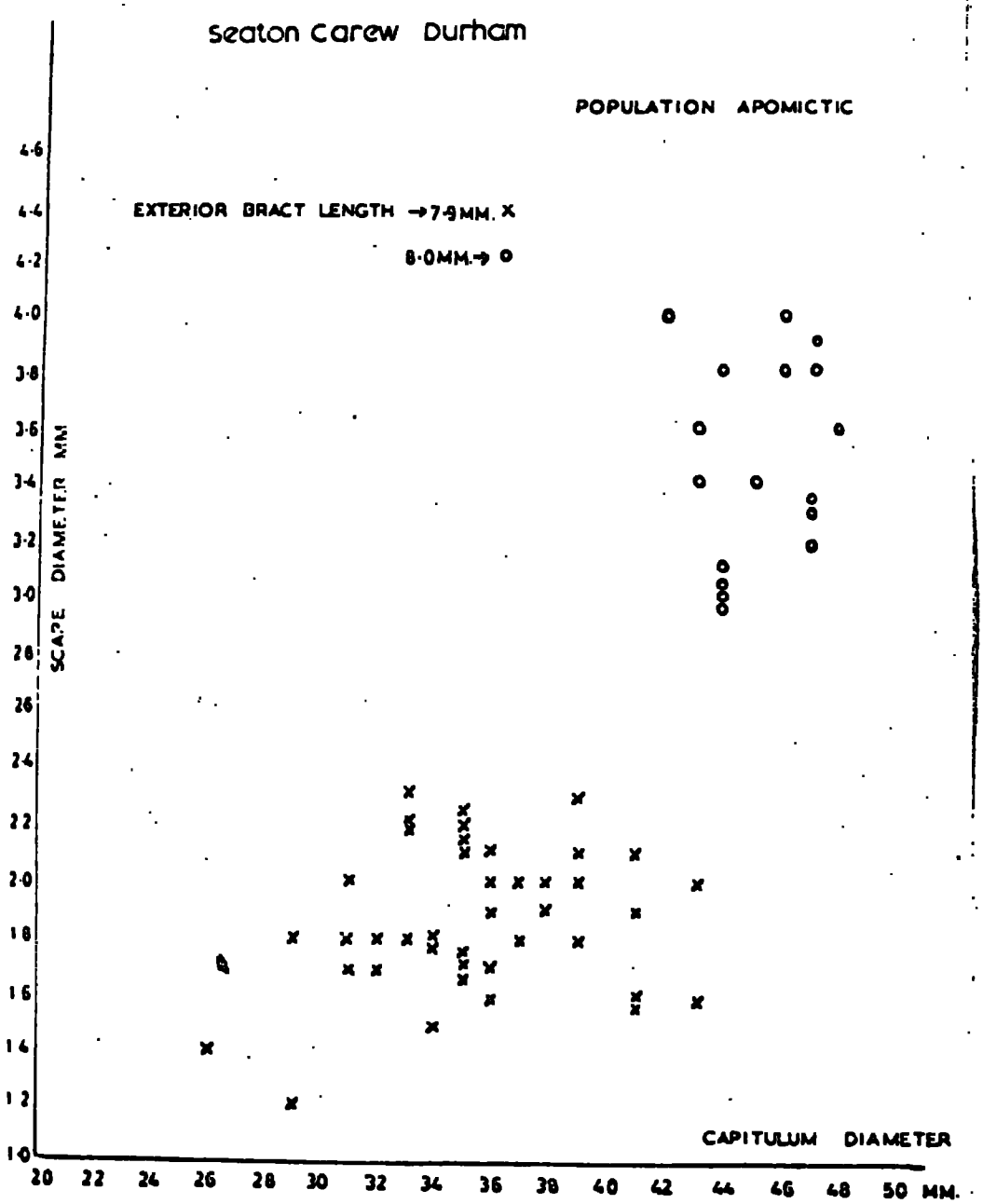

Seaton Carew Durham
POPULATION APOMICTIC
EXTERIOR BRACT LENGTH →7·9MM. X
8·0MM.→ O
SCAPE DIAMETER MM
4·6
4·4
4·2
4·0
3·8
3·6
3·4
3·2
3·0
2·8
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
CAPITULUM DIAMETER
20 22 24 26 28 30 32 34 36 38 40 42 44 46 48 50 MM.

Diagram 12.

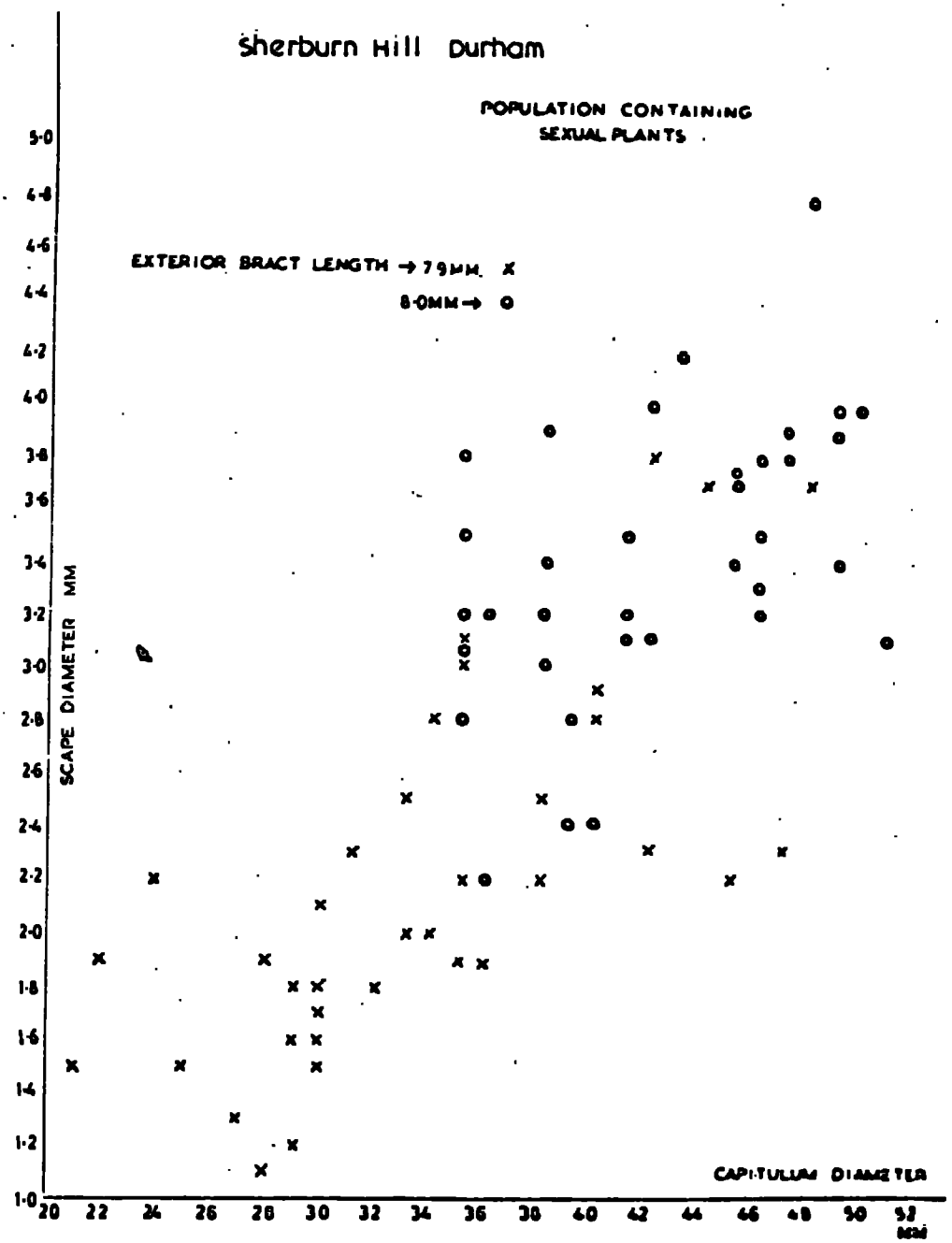

Sherburn Hill Durham
POPULATION CONTAINING SEXUAL PLANTS
EXTERIOR BRACT LENGTH → 7·9MM.
8·0MM →
SCAPE DIAMETER MM
CAPITULUM DIAMETER
5·0
4·8
4·6
4·4
4·2
4·0
3·8
3·6
3·4
3·2
3·0
2·8
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
20 22 24 26 28 30 32 34 36 38 40 42 44 46 48 50 52
MM

Table 33 (con.)

Alnmouth, Northumberland. Grey dune system, dominated by Agrostis stolonifera, but species-rich.

Species present: T.hamatum (Vulgaria)

T.brachyglossum (Erythrosperma)

T.brachyglossum from this station has reductional pollen. Regular or near regular pollen is found in about 10% of this species. T.hamatum has mostly restitutional pollen, and is not suspected of sexuality. No cytology.

Very considerable hybridisation, with over 50% of the individuals showing hybrid characteristics. This presumably occurred through pollination of facultative and sexual T.brachyglossum with partially and totally reductional pollen from T.hamatum.

Bamburgh,Northumberland. A grey dune system, similar to Alnmouth.

Species present: T.hamatum (Vulgaria)

T.brachyglossum (Erythrosperma).

Situation apparently very similar to that at Alnmouth, 15 miles to the south. Regular pollen found in about 12% of T.brachyglossum, and the remainder of this species with reductional pollen. T.hamatum with partially restitutional pollen.

Extensive hybridisation, with at least 40% individuals with hybrid characteristics. T.oxoniense occurs in neighbouring dunes, but does not participate.

Table 33 (con.)

Seaton Carew, Co. Durham. Damp Festuca turf on sand, Agrostis stolonifera turf on slightly saline mud, grey dune system, dominated by Agrostis stolonifera, yellow dune system with Ammophila, Elymus and Agropyron junceiforme, all within a few yards, and all carrying a large Taraxacum population.

Zinc works end;

Species present: T.hamatum (Vulgaria)
T.spilophyllum (Vulgaria)
T.cordatum "
T.cophocentrum "
T.brachyglossum (Erythrosperma)
T.unguilobum (Spectabilia)
T.maculigerum "

The situation here was confused by the richness of the Taraxacum-flora which may have included still more species. The rare Scandinavian Erythrosperma-species T.laetum, T.obscurans and T.scanicum are all recorded from this very interesting locality, and it appears that T.hibernicum and T.serratilobum are among the Spectabilia-species which are also found here.

Neither T.unguilobum or T.maculigerum have pollen, so we can presume that these species were pure-bred.

None of the other species, including the usually facultative T.brachyglossum showed wholly reductional pollen, or regular pollen. No

Table 53 (con.)

evidence for intersectional hybridisation was found (see diagram 12, in which sampling was limited to T.brachyglossum and the Vulgaria-species).

North Gare end.

About ½ mile to the north, in grey dunes, T.brachyglossum occurred alone, well separated from the T.brachyglossum at the Zinc Works end. At the North Gare, 21% of the plants had regular pollen, and the pollen of the rest was reductional. One diploid, and three hyperdiploid plants were found at this locality. No hybridisation was evident, presumably due to the fact that only one species was present. It is of interest that:

1) T.brachyglossum seemed to differ in meiotic behaviour, and thus in breeding behaviour in two neighbouring localities.

2) The rather short distance between the two populations (perhaps 500 metres between outliers of each) seemed sufficient to stop infiltration of reductional genes into the zone of obligate apomicts, and also to stop hybridisation occurring in either locality.

Conclusions about investigations into hybrid populations in the field.

1) Hybridisation may occur between a reductional ovule and a reductional pollen grain. The latter occur, at a low rate, in a greater range of species than reductional (sexual) ovules.

2) Where sexuality is not known to occur, there is no evidence of hybridisation, although no analyses have been made (hybrid populations are readily spotted by eye).

3) All hybrids are seed-bearing. Sexuals, facultative apomicts, and obligate apomicts have all been found in hybrids, with chromosome numbers

from 16 to 33, with 16, 17, 18, 22, 23, 24, 26, 28 predominating (see chapters 8, 9).

4) Apart from the flower characters used in hybrid analysis, all of which seemed to be valid differentiae for the two sections for the species involved, the following characters were also used as differentiae. These came from the achene collections made from the localities investigated:

Length of cone/length of achene.

Width of achene/length of achene.

Achene colour.

Degree of achene spinulation.

Length of rostrum/length of achene.

The first two characters proved to be valuable for separating the sections with the species used. The next two characters are also useful, but do not vary continuously. Length of rostrum/length of achene proved of no value. It would thus be perfectly possible to use achene characters for a hybrid index, always supposing that floral and achene characters could be obtained for the same plant, which is not often possible in the field. Achene characters are less suitable for a scatter diagram, as the range of variability is not very great in the first two characters. Attempts to correlate achene characters with chromosome number on a scatter diagram in a hybrid population, met with a conspicuous lack of success.

5) Sexuality is only known in this country from T.brachyglossum and T.subcyanolepis at present, but only a few populations from a small area of the country are yet known. Regular and reductional pollen have been found

in plants from a number of other areas, and other species may well be sexual in Britain.

6) Although it is possible to determine the parent species without much trouble when intersectional hybridisation is occurring, this may be much more difficult if the hybridisation is intrasectional. So far there is no evidence of intrasectional hybridisation, but a locality has yet to be found where sexuals occur with other species of the same section. Such localities doubtless exist, and intrasectional hybridisation may be of frequent occurrence.

7) When intersectional hybridisation occurs, up to 60% of the population may not be readily assigned to one parent species or the other, and most of these are rather intermediate in sectional characteristics. It is possible that new species may arise through restitutional meioses and obligate apomixis becoming fixed in a hybrid biotype with an evolutionarily successful genotype. In fact, there is no evidence of particular intermediates being very successful in the field as yet, and indeed it seems that most hybrids may be at an evolutionary disadvantage compared with the parents. This is suggested by the apparently high rate of production of hybrids, compared with the integrity of the parental types, introgression being absent. This suggests that the hybrids die out quickly, and for this reason do not backcross much, for they are quite fertile. It is clearly an immediate disadvantage for a sexual plant to be in a position to hybridise, and it may be that this problem has been solved many times in the past by the successful establishment of an apomictic hybrid of evolutionary potential. The reason that no such successful hybrids are found in the

few populations which still have sexuals, and still hybridise extensively to their own detriment, may be that they have not yet arisen, which is why sexuals are still present! One must hope for the future of the genus that all facultative sexuality is not lost in this manner, for despite the great adaptability of the obligate apomicts, they would not be suited to weather a catastrophe such as the occasional radiation storms which apparently are important in changing the biological face of the Earth.

Chapter 12

REVOLUTIONARY TRENDS IN TARAXACUM

In common with the great majority of plant material, it is not possible to use direct (i.e. fossil) evidence in elucidating the evolutionary history of Taraxacum. Nevertheless a great deal of indirect evidence exists which is relevant to this subject, and with the important reservation that it is impossible to be certain whether our interpretation of this evidence is correct, it is possible to make an educated guess as to the more important evolutionary trends in Taraxacum.

In deciding the early history of Taraxacum, it is informative to examine briefly the closest relatives outside the genus. In the tribe Cichoriae there are a number of genera which bear a superficial resemblance to Taraxacum. These include Mycelis, Lactuca, Cicerbita, Cichorium, Crepis, Hieracium and Tragopogon, all genera with a Palearctic distribution, and the majority of which are rather successful. In addition, several of these genera share with Taraxacum the property of agamospermy. Perhaps the two closest widespread genera are Leontodon and Scorzonera, Eurasiatic genera with a centre of origin in the Middle-East. Recently, a new genus, so far comprising two species has been found in Iran. This was discovered during the preparatory work to Rechinger's 'Flora Iranica', and has been named Wendelboa after the discoverer. Wendelboa seems to be intermediate between Taraxacum and Scorzonera and is very close to Taraxacum sect. Rhodotricha in many respects. It differs by a rugose pappus, and other minor characters. Unfortunately, the chromosome number of Wendelboa is not

yet known, but it is known to be sexual. It seems very likely that Wendelboa and the Rhodotricha have evolved very little from the ancient stock which gave rise to the genera Taraxacum and Scorzonera.

As the closest relatives of Taraxacum are sexual and diploid, it is reasonable to assume that the first Taraxaca were also sexual and diploid. Furthermore, it is unlikely that the very great diversity which has evolved in Taraxacum could have arisen from chiefly apomictic stock. It is also reasonable to assume that the genus is monophyletic in origin. For all the diversity exhibited, Taraxacum is a 'natural' group, and all species share a number of diagnostic characters in common (see chapter 1). It is possible to assume that all Taraxaca arose originally from one area, as we shall see later in this chapter.

One of the most striking aspects of the genus to the biosystematist is that in a genus which shows a very complicated relationship in depth between most taxa, a group of sections, very distinct from the rest of the genus, are the only Taraxaca to contain no apomictic members. These sections bear a number of characters in common. These are tabulated in table 32 . Further, it will be noticed from this table that all these sections except the Glacialia are limited to the Middle-East, and are mostly found in Iran, Turkey, Afghanistan, Turkestan, Kadakhstan, the Crimea and Georgia. It is in the centre of this area, in Iran, that Wendelboa is found. There seems very good grounds to suppose that these sections are of a primitive nature; that they are very close to the original representatives of the genus. The Serotina and Leptocephala are mostly sexual sections which also occur in this area, but also further west, into

Diagram 13. In this map, the number of sections occurring in each country is indicated. A black line surrounds those countries in which the majority of the sections are thought to be entirely sexual.

the Mediterranean. These sections have a number of rather less primitive characters, and furthermore they are self-fertile. They seem to represent an early evolutionary advance in the genus. The Glacialia may be a relict of a still earlier advance into the Mediterranean, when the primitive types were more widespread than they are today.

If the number of sections of Taraxacum occurring in each Eurasian country is mapped, as has been done in diagram 13, it is clear that the centre of diversity in the genus coincides with the area in which the primitive types occur, and also with the area in which the greatest portion of sexual sections is known. This finding agrees with the age and area hypothesis of Willis (1925) in the most elegant manner. Indeed, Taraxacum would seem to be one of the most convincing examples which can be used in support of this hypothesis, which has come under considerable criticism.

The evolutionary trends which resulted in the more advanced, chiefly apomictic sections in Taraxacum are bound to have been of a complicated nature, as the genus as we know it today is a very complicated one. I have summarised what I feel to have been likely evolutionary pathways in diagram 14. I have discussed my views on the evolution of polyploidy and apomixis in Taraxacum elsewhere (chapter 8), and these are clearly relevant to the following discussion.

Apart from the primitive sections, there is another obvious discontinuity in the genus. This is the section Laevia. This Arctic-Alpine section is found very sparingly in the high arctic (above the 70th parallel) and also in a few scattered alpine sites in Europe; in Tierra del Fuego, the Falkland Islands, Australia and New Zealand, and probably in various

Diagram 14. Some hypothetical evolutionary pathways in Taraxacum.

AN EVOLUTIONARY SCHEME OF THE WESTERN EURASIAN TARAXACA

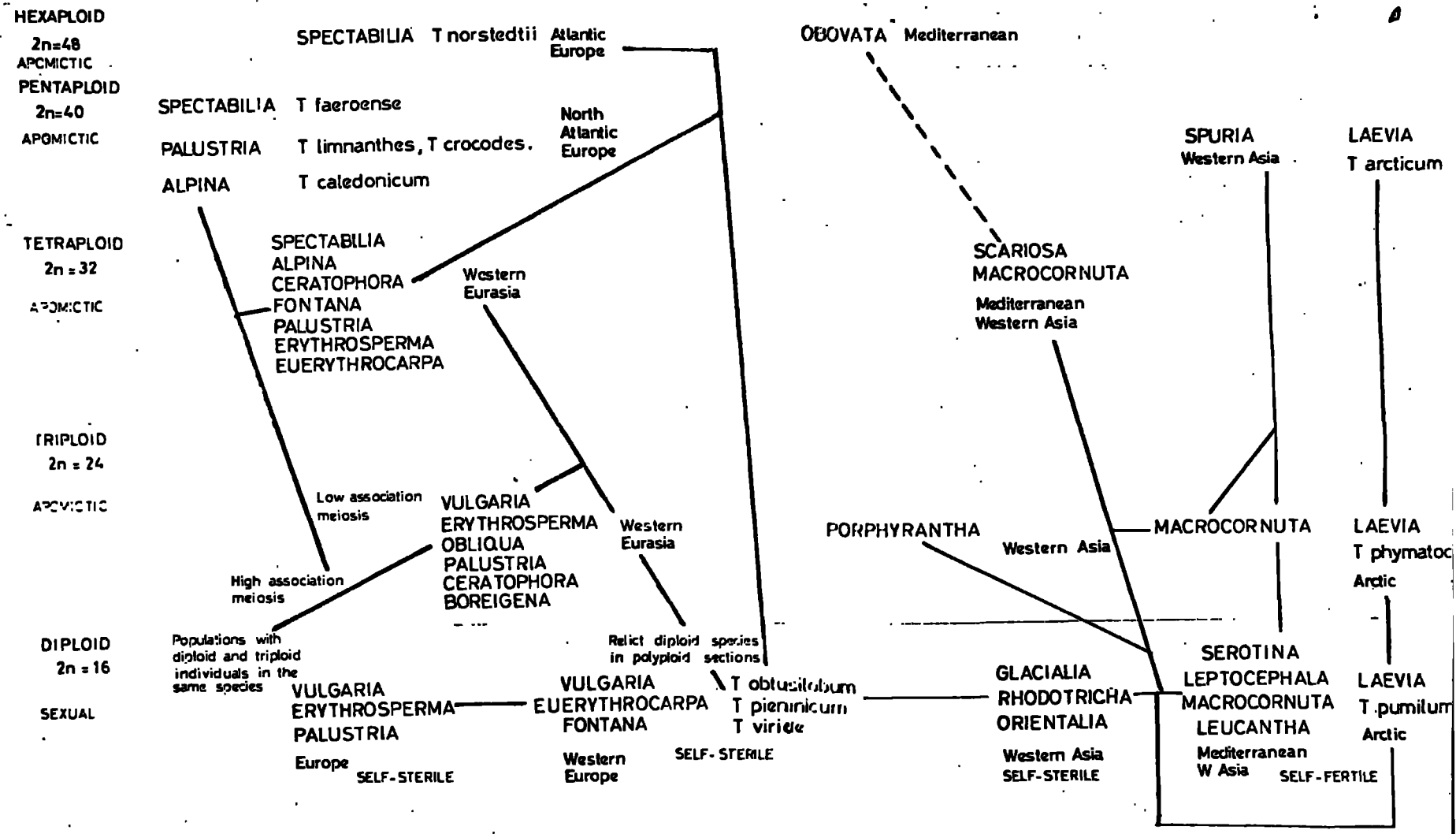


Table 32. The Primitive Sections of Taraxacum

Primitive character	Self-incompatible sections with diploid sexuals only					Other sections
Rostrum to achene absent, or shorter than achene, thick	x	x	x	x	x	0
Achene fusiform	x	x	x	x	x	Laevia
Achene without spines or tubercles	x	x	x	x	x	0
Exterior bract scarious with dark midrib	x	0	x	x	x	Scarious[sa], Palustria
Leaves and scape farinose	0	x	0	0	x	Spuria
Involucre less than 8 mm.	x	x	x	x	x	Leptocephala, Parvula
Exterior bract linear-lanceolate, adpressed	x	x	x	x	x	Spectabilia, Serotina, Leptocephala
Pappus not white	x	x	x	x	x	0
Section	Rhodotricha	Leucantha	Glacialia	Orientalia	Oligantha	
Distribution	W.Asia	W.Asia	S. Europe	W. & C.Asia	W.Asia	

isolated sites in the Andes and Rockies. The very heterogeneous species T.andinum, T.mexicanum, T.scopulorum and T.rupestre probably include some Laevia biotypes, although these names are at present used to cover all montane Dandelions growing in various regions of America. In this problem at least, the Americans are very backward! The Laevia are very individual in appearence, although not particularly primitive, as we understand Taraxacum characters. There is one sexual species in Greenland, T.pumilum. This is a most remarkable place for a sexual species of Taraxacum to occur. Triploidy, tetraploidy and pentaploidy are also recorded in this section. The inference is that this is a very early offshot of the genus, perhaps of Tertiary origin. It is presumed to have migrated north in Asia, and then circum-boreally, and down the Asian and the American mountain chains, thus accounting for its very remarkable discontinuity in the southern hemisphere, which led Dahlstedt, without any other good reason to describe the southern plants as a separate section, the Antarctica. I have included them with the Arctica and the Glabra in Schischkin's section, adapted from Handel-Mazzetti, the Laevia. Van Soest's section from Alpine Europe, the Pachera, pose a difficult problem, as they are intermediate in many respects between the Laevia and more advanced sections. Indeed, they may be of hybrid origin. Nevertheless, they possess a sufficient number of the remarkable characters of the Laevia to be included in this section.

It is probable that the immigration of the self-fertile species of the Mediterranean also occurred before the first glaciation. There seems to be little doubt that this was also a quite separate happening. The main advance of Taraxacum, which gave rise to the bulk of the sections and

species is thought to be correlated with the glaciations. The rapidly shifting open habitats which the post-glacial aftermaths would have created seem to be an habitat in which the evolution of apomixis (a second time, for most of the Laevia species are apomictic) might be of considerable advantage. Handel-Mazzetti (1907), van Soest (1958b) and others have discussed very fully the possible ways in which apomicts might have taken advantage of the glacial environments. It seems that sexual, facultatively apomictic and obligately apomictic plants, evolving rapidly in circumstances of frequent genetic and geographic isolation, followed by remeeting would quite possibly give rise to the very complicated relationship in depth of a very large number of biotypes which is found today. It is clear that in most cases the sections are 'natural' taxa, and they may represent the main hybrid types, from which segregation, recombination, and then later in the obligate apomicts, somatic mutation, gave rise to a relatively small number of successful biotypes, mostly obligate apomicts, which we find today. To have survived this time in the face of inter-and intra-generic competition and to have lived through the very varied climatic regimes which have occurred since leads us to suppose that these biotypes have by virtue of their apomictic properties fixed a very habitat-specific genotype, which might render them very good indicator species for phyto-sociological and phytogeographic studies. Indeed, the Scandinavians have frequently used biotypes in this genus with some success in these fields. That the biotypes are of a very wide distribution in many cases, and very constant both in morphological characteristics, and in ecological requirements encourages us that these species are of age and value, and do

not, as it has been suggested (especially by Fürnkranz 1966) arise anew at the least provocation. It is clear that to a specialist, a hybrid is never recognisable as another biotype. Most Taraxacum species now seem very stable, even in the exceptional circumstances described in chapter 8; although some hybridisation occurs, the hybrids are not very successful.

It is worth examining rather more closely the significance of facultative agamospermy, both in the history of the genus, and at the present day. Whereas most apomicts evolved an asynaptic meiosis, with total restitution, at least in the female meiosis, and thus precluded the possibility of any panmixis for the sake of fixing an advantageous genotype, it now seems that in a number of cases triploidy was not accompanied by such a mutation, and that some reductional gametes are formed. The evolutionary significance of this is considerable. It means that some potential for gene exchange exists, and that the biotypes which possess some sexuality are not doomed to extinction after a major environmental change. (Actually, I feel that the 'tragedy' of agamospermy has been rather overplayed. From present distributions it is clear that most agamospermic biotypes must have survived a tremendous variety of environmental conditions to be extant at the moment. No doubt the great plasticity which has been part of the genetic requirements which have been fixed in many sections, particularly the Vulgaria and Erythrosperma, has helped these plants to survive many regimes, as has the great power of the genus to spread before the wind in the shape of air-borne dissiminules.) Nevertheless, despite the possibilities of somatic mutation, emphasised by Gustafsson (1935), the potential for change in a plant and thus the chance

that the genus will be substantially different in, say, 50,000 years is greatly increased by the presence of facultative apomixis. It is of the greatest interest to enquire how the facultative plants, which must waste a greater proportion of reproductive material than the obligate apomicts, manage to survive in competition with the apomicts. It may be the phenomenon of heterosis, as I have heard suggested, as there is some evidence that the apomicts are rather heterozygous. There is no evidence to suggest that the obligate apomicts are less vigorous. We do not know the answer to this problem, but if I was asked to guess the reason, I would suggest that the cause is the very great habitat specificity of the species. In most places, it is most unusual to find more than 2-3 species occurring within pollinating range of one another, and these are usually obligate apomicts. In fact, I suspect that the facultative plants are not often in competition with obligate apomicts, although we have seen in chapter 9 that this does occur at times, with considerable interspecific gene-flow resulting. It would be of the greatest interest to investigate whether there is a bias for facultative species to grow with facultative species rather than obligate ones; or by themselves. It certainly seems to be true that hybridisation is an uncommon phenomenon today. In the past, perhaps especially in the late-glacial, it may have been very much more frequent, before habitat types stabilised.

If we examine the apomictic sections, we find that they divide into three broad categories:

1) Those possessing a number of primitive characters (those possessed by the sexual Asian sections in Table 14), restricted to central Asia, with

a number of sexual species. Examples: Macrocornuta, Kashmirana, Tibetana, Mongolia, Eu-Erythrocarpa, Scariosa (the last two also found in S. Europe- apparently a well-worn migratory path).

2) Those with no, or little sexuality recorded, and few primitive characteristics, but with a very widespread, almost circumboreal distribution Example: Ceratophora. (The Laevia, almost certainly an earlier advance with very individual characteristics, have a very similar biological situation to this section).

3) Those with little or no sexuality recorded, and few primitive characteristics, but with a local distribution, often on the Western, or Eastern sea-boards of Eurasia. Examples: Vulgaria, Spectabilia, Palustria, Erythrosperma, Sinensia, Calanthoidia and most of the rest. The most advanced, youngest sections.

It is thought that group 1 evolved, perhaps coincidentally with apomixis, in Asia during the glaciations, and spread westwards and eastwards, perhaps during an interglacial, to situations in which they are now sometimes found in isolated and apparently relict stations as far apart as Poland and the Kuriles (both sexual species). Apomixis has evolved in all these groups, which clearly were the forerunners for groups 2 and 3, which are today much more successful. Perhaps at the same time, one of these types, probably the Macrocornuta, gave rise to a very successful group of obligate apomicts adapted to Arctic conditions, which must have overrun the Northern Hemisphere during an early interglacial (but not this one?). These are group 2, the Ceratophora, unsuccessful relicts in Eurasia now, but very successful in Arctic America, where no later advance

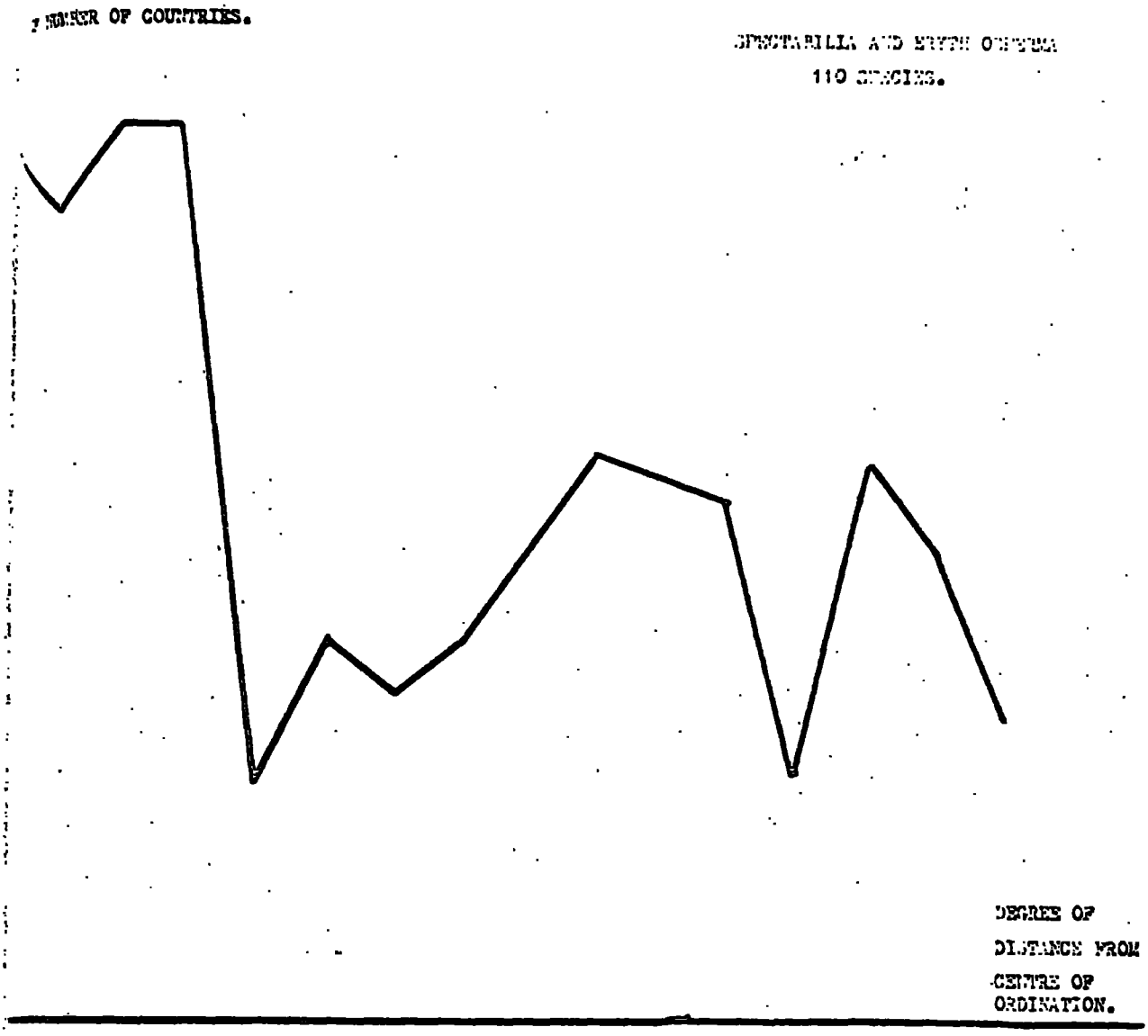
has reached. They may have outcompeted the Laevia, an earlier advance, which are now very scarce there. A few Spectabilia occur in S.E. Greenland in fact, but these are all Icelandic or Scandinavian species, and may be there due to long distance dispersal, and, or introduction by human agency.

Group 3 arose, it is suggested, from group 1. Some sections are very widespread, the Erythrosperma for instance which occurs from Iceland to Persia. Others are very localised, and some of these are undoubtedly of a recent origin; the Boreigena for instance, confined to Scandinavia, may be the result of hybridisation between the Vulgaria and Spectabilia in situ. Others may be much older. The Obovata, for example, may indeed have arisen from the second Mediterranean advance of the inbreeding sexuals. They are now restricted to the Western Mediterranean - an unique distributional type, and may be even older than the widespread Erythrosperma which are clearly a successful off-shot of the Eu-Erythrocarpa. It has already been suggested that the Boreigena have a hybrid origin. Van Soest has suggested that other sections may be of hybrid origin. The Spectabilia and Fontana, for example, which he suggests may be the result of crossing between the Vulgaria and the Palustria and Alpina respectively. In support, it must be said that the latter three sections are much more widespread than the former two, and thus may be older. But here we enter the realms of pure speculation. In the post glacial melting-pot, many types of hybridisation must have occured between the young species, and it is not very profitable to try to trace the evolutionary paths more closely.

This becomes even more true with the evolution of species. It did occur to me to carry out one more simple test on the age and area

hypothesis. In chapter 4, it is related how the numerical taxonomy of the larger apomictic sections revealed a relationship in depth, with some species showing a much higher mean resemblance to species in the same section than others. Those species with a higher mean coefficient of similarity are ordinated to the centre of these numerical taxonomies, and those with a low mean resemblance gravitate to the outside. Reference to diagrams 1 and 2, showing ordinations of species in the Palustria and Spectabilia illustrate this point. It seemed to me that those species with a high mean coefficient of similarity may be closer to the root of the section than those with a low mean similarity, I envisage a theoretical model which may perhaps be best represented by a tree. A 'core' of species arise from the ground, and as time goes on radiate from this centre, the tree-trunk, adaptively, to form rather dissimilar species on the most distant twigs. In the meantime the original species, little changed, continue to progress up the centre of the tree, giving rise to more branches as it goes. I thought that the species which had evolved furthest from the central trunk, those of low mean similarity, might be reasonably expected to be those which had become particularly adapted to a very specific environmental regime. These species might be the youngest, much younger than the relatively little unchanged central core, and, according to the Willis hypothesis, with a much more limited area than those species with a high similarity. In diagrams 1 and 2, the ordinations for the Palustria and Spectabilia and also the ordination of the Erythrocarpa s.l., which I do not present here for practical reasons, I designated a scale of 1-17 to indicate the distance from the centre of the ordination

each species was placed. A reading was then recorded of the mean number of countries that all species in each class on the scale occurred in these three ordinations, and the class on this scale was plotted against the mean number of countries in which this class was found. This is shown on graph 5. It will be seen that there is a broad tendency for the number of countries in which the class is found to decrease, the further from the centre of the ordination the class is situated. In other words, the lower the mean coefficient of similarity that a biotype possess, the less its area of distribution. If we assume that those species which are more dissimilar are of a more ~~recent origin~~ advanced nature, this result ~~also~~ dis agrees with Willis's age and area hypothesis.



Graph 5. The number of countries in which species of the Spectabilia, Palustria and Erythrocarpa s.1 occur, plotted against the distance from the centre of ordinations at which they occur.

Appendix 1

CYTOLOGICAL TECHNIQUES

Root-tip squash for mitosis

In order to find a satisfactory method of examining somatic chromosomes in Taraxacum, the use of a number of different techniques was tried. I wished to achieve the following results:

good staining of chromosomes;

good spreading of chromosomes;

avoidance of overcontraction of metaphase chromosomes;

well emphasised chromosomal constrictions;

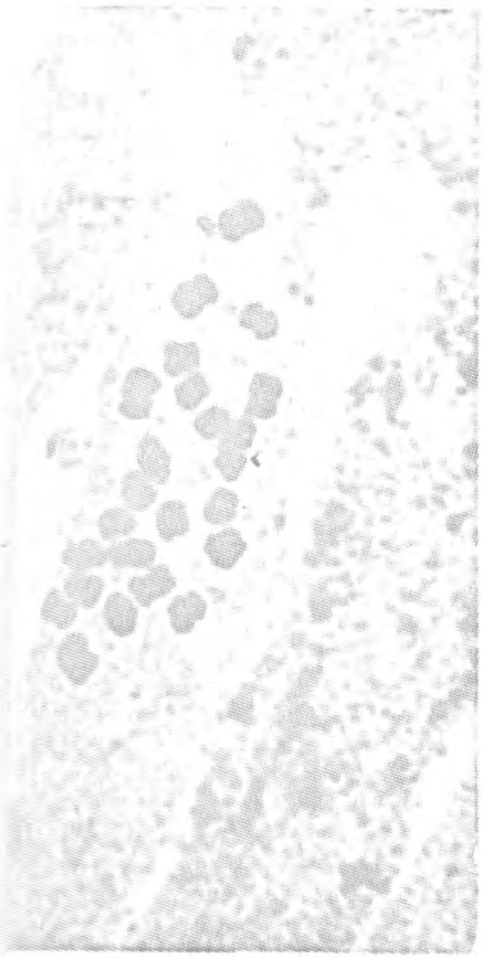
and a satisfactory number of metaphase plates.

To stain the chromosome, I tried aceto-orcein, aceto-carmine, with a mordant of ferric chloride, and Feulgen's stain. The quality of the staining using the first two reagents was very poor, but excellent results were achieved with the use of Feulgen. The preliminary hydrolysis used in this technique also enhanced the spreading of the chromosomes. With this technique, the chromosomes were not overcontracted, but chromosomal constrictions were unfortunately not very evident. To attempt to increase the clarity of the constrictions, various pretreatment techniques were employed. It was also hoped that the use of these techniques would increase the number of metaphase plates by damaging the spindle and thus delaying the mitotic process at the metaphase stage. The following drugs were tried at 20°C and at 1°C:

Colchicine	2 hours, 3 hours and 4 hours at 0.15%
a-bromonaphthalene	" saturated solution
8-hydroxyquinoline	2 hours, 4 hours, 6 hours, 0.002 mol.aqueous solution.
paradichlorbenzene	2 hours, 3 hours, 4 hours, saturated solution.

Most of these methods were useless, with few or no metaphase plates being found, and those that were seen were of an inferior quality, often showing highly distorted chromosomes. It was not found possible to avoid chromosomal fragmentation when using colchicine. Only the preparations using paradichlorbenzene as a pretreatment showed any real promise. At 2 hours at 20°C (no cold treatment samples showed any division at all), the number of metaphase plates found was high, perhaps 50% more than in root-tips without pretreatment. Furthermore the chromosomal constrictions are very clear when paradichlorbenzene is used. Unfortunately, this drug seems to contract Taraxacum chromosomes, and this obscured all differential length factors (see photographs 37, 38). In conclusion, a satisfactory technique for the study of chromosome morphology could not be found, and it appears that the perusal of many plates, after the manner of Guðjónsson (Chapter 7) may be the only practical method.

It was found that root-tips fixed in the field, or from pots in which the plant had been growing for over a month showed very little mitosis. I discovered that the most convenient manner of obtaining rapidly dividing roots was to germinate achenes on filter paper and excise the young radicles 8–16 hours after emergence. Several satisfactory metaphase plates could then be found in an average preparation, and upwards of 10% of the



Photographs 37 and 38. The effect of pretreatment with paradichlorbenzene on root-tip squash preparation; T.undulatum, 2n=24; T.faeroense. 2n=40.

x 3000

x 1500

meristematic cells could be found in division. The time of day of fixation did not appear to be important. The drawbacks in this technique were:

chromosome counts were obtained from abnormal individuals which would not reach maturity;

excising the radicle killed the plant so that the development and behaviour of the plant examined could not be followed.

In fact chromosomal abnormalities were not found to be very frequent (chapter 6) and the counts obtained by this method were probably fairly representative. In breeding experiments it was often found to be necessary to know the karyotype of an individual, and this was achieved by the following means: repot the individual in a plastic pot filled with John Innes compost No. 3, and maintain a high water level by submerging the pot in water to a depth just at soil level. Place in a heated and lighted greenhouse and excise the roots in 14-21 days. This technique is specially effective if the plant had previously been growing outside as a small semi-dormant rosette, as is found in winter or late summer. Good numbers of dividing cells can usually be found.

A schedule for the cytological technique used follows:

1. Fix in a 3.1 mixture of absolute ethanol and glacial acetic-acid for 24 hours. If kept longer than a week, place in a deep freeze. Examine within 2 months.
2. Hydrolyse in N/10 HCl for 7-8 minutes at 60°C.
3. Stain in Feulgen's stain for 1-2 hours (see below for a recipe for the stain).

4. Excise the stained tip of the radicle onto an alcohol-cleaned slide, and mount a cover-slip over aceto-carmine.
5. Tap the cover-slip to separate cells, squash with thumb under filter-paper, and then tap vigorously over the filter-paper with the handle of a dissecting needle.
6. Examine under a microscope, and tap further if cells not completely flattened.
7. After examination under the x 100 microscope objective, including counting, drawing and photography of suitable plates, place slide, cover-slip uppermost, on solid CO2 (proprietry name Cardice).
8. Leave slide on the dry ice for a minimum of 2 minutes, then remove, and lever off cover-slip with the edge of a safety razor-blade.
9. Place slide in 3.1 acetic-alcohol for 5 minutes.
10. Mount new cover-slip over 'Euparal'. Leave to harden for 48 hours.

Coordinates, counts and the reference number were attached to the permanent slide so created. For results of these preparations, of which about 1000 were made, see appendix 4.

All microphotographs, including all those in this thesis were made with a Leitz 'Orthomat', with automatic attachment, using 'Microneg.Pan' film, A.S.A. speed 6. All photographs of chromosomes were taken using the x100 oil-immersion objective. Other photographs in the thesis were taken with an Exacta II.

Examination of pollen mother cells for meiosis

A number of fluids were again tried as possible agents for the staining of the meiotic chromosomes of Taraxacum. Some success was obtained with aceto-orcein, aceto-carmine mordanted with ferric chloride, and with Feulgen. The staining was much clearer using Feulgen in the majority of cases,, and this was generally used. Examination of tetrad development and pollen size and contents was made with aceto-carmine, mordanted with ferric chloride. This is quite adequate for this purpose, and is much quicker than the Feulgen technique. The schedule used for male meiotic preparations follows:

1. Excise buds when about 5 mm. high. Squeeze bud with fingers to allow penetration of the fixative.
2. Fix in 3.1 acetic-alcohol (as for root-tips, see above).
3. Hydrolyse in n/10 HCl for 7-8 minutes at 60°C (as for root-tips).
4. Stain in Feulgen's solution (for method of preparation, see above).
5. Excise 2-3 florets, and macerate in aceto-carmine. Remove excess debris, and squash under cover-slip with filter paper onto alcohol-cleaned slide.
6. Examine under microscope. If no meiotic stages are present, it is unlikely to be profitable to continue to investigate that particular bud, as all the florets in the bud perform male meiosis simultaneously.

Embryology

Two embryological stages were of particular interest to me (see Chapter 5). These were female meiosis, and the early stage of embryo development. Valentine and Maxwell (1966), working in the same department

were using a new embryological technique in Primula, which involves softening of the cell wall by dissolving the calcium pectate of the middle lamella with a pectinase solution, thus allowing the tissues to be readily dissected with a mounted needle. The object of this technique is to bypass the tedious processes involved in paraffin wax sectioning. Furthermore, the technique may be superior to sectioning for some purposes, as whole organs (such as the embryo and endosperm) can be examined, and accurate cell counts made. It seemed that this technique might be suitable for embryological examination in Taraxacum, and indeed a slightly modified method proved satisfactory for discovering whether embryos had formed precociously in the ovule of Taraxacum. The schedule for this technique follows:

1. Fix heads in 3.1 acetic-alcohol, squeezing the buds to allow penetration of the fixative. Female meiosis occurs when the bud is 9-10 mm. high. For examination of precocious embryos, fix about 24 hours before anthesis.
2. Digest buds in a saturated solution of pectinase in water, with about $\frac{1}{5}$ volume of N/10 HCl at room temprature for 24 hours.
3. Stain the heads in Feulgen's solution (see above) for 3-4 hours.
4. Dissect out ovules with the aid of entomological needles mounted in glass, under a dissecting microscope.
5. Mount under water, and examine under a microscope. Slight pressure on the cover-slip may often split the ovule to reveal the embryo-sac.
6. To make the preparation permanent, remove cover-slip, and dry slide on a warm surface (a radiator was used) for 24 hours. Pass slide through 3.1

acetic-alcohol (3 minutes) and mount a cover-slip over Euparal. Examples of the results of this technique may be found in photographs 5 and 9.

It was found that earlier embryological stages could only be properly examined through the use of paraffin wax sections. A rather standard technique was used with considerable success, and a rather small amount of work using this technique provided excellent examples of most of the stages of embryo-sac development, including female meiosis (see photographs 4, 6, 7, 8). It will be of great value to use this technique much more in subsequent work (see chapter 5). A schedule follows:

1. Fix heads as for the dissection technique.
2. Place heads in absolute alcohol (8 hours).
3. Place heads in 1.1 absolute alcohol/chloroform (2 hours).
4. Incubate heads at 30°C for 2 days in chloroform, and increasing amount of paraffin wax.
5. Incubate heads for 5 hours at 60°C in 2 parts wax to one part chloroform.
6. Immerse heads in melted paraffin. Cool.
7. Cut wax blocks containing heads to rough cubes, and mount on the microtome, having exposed the region to be sectioned with a pen-knife.
8. If the sections are unsatisfactory, wet blade and wax.
9. Place sections shiny side down on a wet slide.
10. Dry the slide on a warm surface for 24 hours.
11. Run the slide through the following fluids in staining jars:
    xylol (5 minutes); absolute alcohol (2 minutes); 50% ethanol (5 minutes) N/10 HCl at 60°C (6 minutes); Feulgen's stain (2 hours); water (1 minute

45% acetic acid (5 minutes) and 3.1 acetic-alcohol (5 minutes). Mount in Euparal.

Preparation of the Feulgen stain

1. Pour 400 ccs. of boiling distilled water over 2 gms. of basic fuchsin.
2. Filter the solution.
3. Add 30 ccs of N/10 HCl, 15 gms. of sodium metabisulphate, and a quantity of decolourising carbon to the solution in a stoppered bottle.
4. Shake the mixture vigourously, allowing the SO_2 to escape. When the bubbles in the black mixture lose their violet tinge, filter.
5. Store the resulting colourless solution of basic fuchsin in SO_2 water in a tightly stoppered bottle in a dark, cool room, preferably a cold-room. It does not mind being frozen.

Technique employed in the colchicine induction of polyploidy in Taraxacum

1. Germinate some achenes, and determine through the root-tip squash method (Q.V.) the chromosome number of the seedlings.
2. If the seedlings prove to be diploid, treat the majority as below, keeping a number as controls.
3. Transplant the seedlings to soil trays (see Chapter 3).
4. When the cotyledons have opened out, and the apical bud is just barely discernable to the naked eye, apply two drops of a 0.2% solution of colchicine to the apical bud, allowing the drop of liquid to rest between the cotyledons, and to dry in this position. Repeat 3 times at 2 hourly intervals on two successive days. Do not water in the interim.
5. The manner by which the surviving seedlings can be examined for

tetraploidy is described in chapter 8.

References:

Darlington C.D. and La Cour L.F. (1962). 'The Handling of Chromosomes'.

Evans A,M. (1955). 'The production and identification of polyploids in two Clovers and Lucerne'. New Phytologist, 54, 2, p. 149.

Valentine D.H. and Maxwell C. (1966). 'A dissection technique for embryo-sacs'. New Phytologist, 65, pp. 75-76.

Appendix 2

SPECIES MENTIONED IN THE TEXT

Genera:

Antennaria Gaertn.

Cardamine L.

Cicerbita Wallr.

Cichorium L.

Crepis L.

Festuca L.

Hieracium L.

Lactuca L.

Leontodon L.

Mycelis Cass.

Poa L.

Scorzonera L.

Taraxacum Weber.

Tragapogon L.

Wendelboa Rechinger.

Species:

Agrostis stolonifera L.

Festuca ovina L.

Poterium sanguisorba L.

Taraxacum Weber

Section:	Species:
Alpestria vS 1966a.	graiense vS1961a
	aestivum vS 1959
	rufocarpum vS 1959

Section:	Species:
Alpina Hgl. 1950	apenninum (Ten.) DC em.vS 1959
	carinthiacum vS 1959
	helveticum vS 1959
	kalbfussii HM 1923
	oreophilum Hgl. 1950
	panalpinum vS 1959
	parsennense vS 1959
	pseudofontanum vS 1959
	vernelense vS 1959
	vereinse vS 1959
Boreigena Hgl.in Hgl. and Lil. 1941	
	cochleatum Dt et Lindb.in Dt. 1912
	macrocentrum Dt. 1912
Calanthoidia Dt. 1926b.	
Ceratophora Dt. 1928	alpicolum Kitam, 1933
	arctogenum ?
	brachyceras Dt. 1906b
	cornutum Dt. 1906b
	deliviosum Hgl.?
	ecorniculatum Hgl.?
	gallicum vS 1961a
	hjeltii Dt. 1912
	hultenii Dt. 1926a.
	lacerum Greene 1901
	lactucaceum Dt. 1928
	macilentum Dt. 1906a
	malteanum Dt. Hgl. 1943
	krattlii vS 1959
	norvegicum Dt. 1906a
	perlatescens Dt. 1926a
	platyceras Dt. 1926a

Section:	Species:
Ceratophora Dt. (con.)	pseudonorvegicum Dt. in Hgl. 1943
	russeolum Dt. in Hgl. 1943
	shikotananse Kitam. 1933
	simulum Brenn. 1907, em. Dt. 1930
	tornense Fries 1908
	umbrinum Dt. in Hgl. 1943
Coronata HM 1907	
Cucullata vS 1959	cucullatum Dt. 1907a
	tiriolense Dt. 1907a
Dissecta vS 1966a	
Erythrosperma Dt.em.Lindb. 1946	
	agaurum vS 1956a
	argutum Dt. 1929b
	austriacum vS 1966b
	brachyglossum Dt. 1921b
	disseminatum Hgl. 1947
	dissimile Dt. 1911
	dunense vS 1956a
	falcatum Brenn. 1907
	friesii Dt. 1921b
	fulviforme Dt. 1923b
	fulvum Raunk. 1906
	isophyllum Hgl. 1938c
	isthmicola Lindb. 1908
	lacistophyllum Dt. in Raunk. 1906
	oxoniense Dt. 1923b
	parnassicum Dt. 1929a
	proximiforme vS in vS and Lamb. 1962
	pseudolacistophyllum 1926b
	ruberulum Dt. and Borgv. 1932
	rubicundum Dt. in Raunk. 1906
	silesiacum Dt. in Hgl. 1938c

Section:	Species:
Erythrosperma (con.)	simile Raunk. 1906
	sqamulosum vS 1957a
	stenospermum Sennen 1925 (vS 1954a)
	taeniatum Hgl. 1942.
	tanylobum Dt. 1933
	tenuilobum Dt. 1909
	tortilobum Florstr. 1914
Eu-Erythrocarpa Dt. 1929	amborum Hgl. 1932
	breviscapum AJR.n.sp.
	fedtschenkoi HM 1907
	pieninicum Pawl. 1924
	pseudocalocephalum vS 1960
	spinulosum vS 1960
Fontana vS 1959	aurantellum vS 1959
	corsicum vS 1959
	fontanicolum vS 1959
	fontanosquameum vS 1959
	fontanum HM 1907
	peralatum vS 1959
	silvicolum vS 1959
	viride AJR,n.sp.
Glacialia HM 1907	
Kashmirana vS 1963	dentisquameum AJR.n.sp.
	fulvobrunneum vS 1963
	gulmargense vS 1963
	vulpinum vS 1963
Laevia (HM) Schischk.em.AJR	andinum Dt. 1907d
(inc.Antarctica HM 1907,	arcticum (Trtv.) Dt. 1905
Pachera vS 1954, Glabra Dt.1928)	dovrense Dt. 1928
	glabrum DC 1838
	handelii Murr 1904
	nevadense Lindb. 1932

Section:	Species:
Laevia (con.)	litanderi vS 1957a
	pacheri Schultz 1838
	phymatocarpum Vahl. in Hornem. 1840
	pumilum Dt. 1905b
	reichenbachii Huter in Murr 1901
	rupestre Greene 1901
	scopulorum Rydb. 1901
Leptocephala vS 1954c	bessarabicum (Hornem) HM 1907
Leucantha vS 1963	leucanthum Ledeb. 1844
Macrocornuta vS 1960	bicorne Dt. 1905b
	brevicorniculatum V. Korol. 1940 (see Kom. 1964)
	kok-saghyz Rodin 1933 (see Krotov. 1945)
	microspermum Schischk 1937 (see Kom. 1964)
	monochlamydemeum HM 1907 em. Hgl. 1938b
	multiscaposum Schischk. 1937 (see Kom. 1964)
	neolobulatum vS 1960
	walichii DC 1838
Mongolica Dt. 1926b	mongolicum HM 1907
	platycarpum Dt. 1907a
Obliqua Dt. 1921b	obliquum (Fried) Dt. 1905
Obovata vS 1954a	obovatum DC 1838
Oligantha vS 1963	oliganthum HM 1907
Orientalia HM 1923	stevenii (Sprengel 1826) DC 1838 em. HM 1907
Palustria Dt. 1928	albanicum vS 1965a
	alsaticum vS 1965a
	apiculatum vS 1965a
	austriniforme AJR n.sp.
	austrinum Hgl. 1946a
	balticum Dt. 1905
	bavaricum vS 1965a
	brachysquameum vS 1965a
	carniolicum vS 1965a

Section:	Species:
Palustria (con)	ciliare vS 1965a
	crassiceps Hgl. in vS 1965a
	crocodes Dt. 1907
	decolorans Dt. 1925
	delanghii vS 1965a
	divulsifolium vS 1965a
	dolomiticum vS 1965a
	egregrium Markl. 1938
	frisicum vS 1956a
	fuornense vS 1965a
	gelricum vS 1965a
	germanicum vS 1965a
	heleonastes Hgl. 1950
	hoedicense vS 1965a
	hollandicum vS 1942
	huterianum vS 1965a
	illyricum vS 1965a
	limnanthes Hgl. 1946a
	lividum Petermann 1849
	murbeckianum Hgl. 1939
	neo-allenii vS 1965a
	olivaceum vS 1965a
	pollichii vS 1965a
	suecicum Hgl. 1942
	tenuifolium (Hoppe) Koch 1840
	turfosum (Schultz-Bip.) vS 1961a
	vestrogothicum Dt. 1910b
Parvula vS 1963	
Porphyrantha (Schischk.) AJR	
	porphyranthum Boiss. 1875
Rhodocarpa vS 1954c	(rhodocarpum Dt. 1907a = schroeterianum)
	schroeterianum HM 1905

Section:	Species:
Rhodotricha HM 1907	kotschyi vS 1966a
Scariosa HM 1907 em.Dt. 1929a	
	aleppicum Dt. 1929a
	apollonis Dt. 1929a
	bithynicum DC 1839
	cyprium Lindb. 1946
	delphicum Dt. 1929a
	graecum Dt. 1929a
	hellenicum Dt. 1929a
	hybernum Stevens 1856
	megalorrhizon (Forsk) HM 1907
	merinoi vS 1954b
	minimum Guss. em. Dt. 1929a
	scolopendrinum Dt. 1929a
Serotina vS 1954a	haussknechtii Uechtr. in Haussk., 1895
	pyropappum Boiss. et Reuter 1842
	serotinum Poiret in Lamarck, 1816
Sinensia vS 1963	bicolor (Turcz.)Dc 1838
	vepallidum Hgl.?
Spuria DC 1838	montanum (Meyer) DC 1838
	syriacum HM 1906
Tibetana vS 1963	mitalii vS 1963
	sikkimense HM 1907

Section Spectabilia Dt. 1930a

(incl. sub-sections Crocea (M.P.Ch) AJR, Naevosa (M.P.Ch) AJR, Eu-Spectabilia (M.P.Ch) AJR and Norstedtia AJR)

acidodontum Dt. 1928
adpressum Dt. 1912
akransense M.P, Ch. 1942
atroplumbeum Dt. 1923a.
britannicum Dt. 1926c
caledonicum AJR n.sp.
calanthum Dt. 1930
cimbricum Dt. in Raunk. 1934
craspedotum Dt. 1923a
croceum Dt 1905a
cymbifolium Lindb. in Dt. 1930b
euryphyllum Dt. 1918
eximium Dt. 1912
faeroense Dt. 1923a
firmum Dt. 1912
fulvicarpum Dt. 1927
hibernicum Hgl, 1935a
hilare Dt. 1923a
hygrophilum vS 1956a
kolaense Lindb. 1926
landmarkii Dt. 1923a
larssonii Dt. 1912
leptolepis M.P.Ch. 1942
leyroi vS 1954b
maculigerum Lindb. 1908
medioximum Dt. 1912
naevosiforme Dt. 1912
naevosum Dt 1908
norstedtii Dt. 1911
obtusatum Dt. 1912
polium Dt. 1911
praestans Lindb. 1908
pseudo-norstedtii AJR n.sp.
purpuridens Dt. 1912
pycnostictum M.P.Ch. 1942
repletum Dt. 1912
rhodolepis Dt. 1911
rhodoneuron Dt. 1912
rubiginosum Dt. 1912
sagittifolium Dt. 1912
scotolepis Dt. 1912
selenophorum M.P.Ch. 1942
serratilobum Dt. 1927
shetlandicum Dt. 1927
spectabile Dt. 1905a
strictophyllum Dt. 1912
unguilobiforme Dt. 1933b
unguilobum Dt. 1912

Section Vulgaria (inc. section Subvulgaria M.P.Ch. 1942) Dt. 1918

acutangulum Markl. 1925
bracteatum Dt. 1925
cordatum Palmgren 1910b
crispulum Hgl. 1934
croceiflorum Dt. 1910a
cyanolepis Dt. 1911b
dahlstedtii Lindb. 1908
dentilobum vS 1954b
duplidentifrons Dt. 1929b
duplidens Lindb. 1908
ekmanii Dt. 1911
fasciatum Dt 1906b
flavescens Hagl. 1943a
haematopus Lindb. 1908
hamiferum Dt. 1928b
helianthum vS 1963
hamatum Raunk 1906
involucratum Dt. 1910
klingstedtii Sonck. 1964
laciniosifrons Dt. 1935
latissimum Palmgren 1910b
litorale Raunk. 1906
interruptum Dt.
laeticolor Dt. 1906b
longisquameum Lindb. 1908
melanthoides Dt. 1935
microcarpum Lindb. 1932
mimulum Dt. in Lindb. 1908
multifidum Hgl. 1934
obtusilobum Dt. in Hgl. 1935
oreinicolum vS 1966b
parvuliceps Lindb. 1909
patens Dt. 1905a
pectinatiforme Lindb. 1908
plicatum Dt. 1933
polyodon Dt. 1910a
pseudohamatum Dt. 1931
retroflexum Lindb. 1909
rhaeticum vS 1959
sellandii Dt. 1923a
semiprivum Dt. 1928b
speciosum Raunk 1906
subcyanolepis M.P.Ch. in Raunk. 1934
sublaeticolor Dt. 1925
stenoschistum Dt. 1910a

Incertae sedis:

laevigatum (Willd) DC 1813
lanceolatum ?
mexicanum DC 1838
nigricans Reichenbach, 1830
officinale Roth. 1793
palustre Dt. 1905
robustum ?
samuelssonni Dt.?
scaturginosum ?

I also possess a full list of Taraxacum-species with theirreferences. The bulk and subsequent cost of publishing this seemed to off-set the need for such a list in this thesis (there are over 2000 names listed). Such a document is of great value however, and I hope it can be published at a future stage.

Appendix 3

PERSONAL CHROMOSOME COUNTS IN TARAXACUM

The numbers quoted in brackets after the species names are my reference numbers, and are included for my own convenience;

The date of collection of achenes, the locality in which they were collected, the nature of the locality, and the collector are given as far as is possible;

Where material was collected as a living plant, this is indicated by the words 'as root'. All other material was obtained as seed, germinated as described in chapter 2, and the chromosomes counted as described in appendix 2;

Numbers followed by S, refers to the number of chromosomes bearing satellites observed; numbers followed by B, likewise refers to the number of supernumerary chromosomes observed.

Altogether 168 counts in 93 species belonging to 19 sections are recorded. The 100 or so chromosome counts from Durham populations, the results of which are outlined in chapter 6 are not included, as most of the plants have not yet flowered.

Chromosome counts have only been recorded where the material has been grown to flowering in the greenhouses at Durham and the herbarium material made from these plants has been verified by Prof. van Soest of the Hague. All voucher specimens have been deposited in the herbarium of Oxford University.

A standard requirement of all counts is that at least 2 readily

analysable metaphase plates from at least 2 seedlings shall have been examined for each recorded count.

Section Rhodotricha

T.kotschyii (548)	2n=16 + 0	Shibilake, Ajerbuijan, Iran, R.H.S. 1966 (P.F.9086)

Section Oligantha

T.oliganthum (549)	2n=16 + 0	Elburz Mts., Iran, R.H.S. 1966 (P.F. 9054)

Section Orientalia

T.stevenii (91)	2n=16 + 0	Ex. Botanical gardens, Moscow, 1965

Section Serotina

T.serotinum (107)	2n=16+ 0	Source unknown 1965
(145)	2n=16 + 0	Ex.Roumania 1964
(189)	2n=16 + 0	Ex. Jasi Botanical Garden, Roumania, 1965.
(438)	2n=16 + 0	Ex. Bucharest Botanical Garden, Roumania 1965
T.haussknechtii (545)	2n= 16+ 0	North of Ezerum, Iran, R.H.S. 1966 (P.F. 9161)

Section Leptocephala

T.bessarabicum (92)	2n=16,n=8	Ex Botanical Garden, St. Andrews, 1964 (as T.bicorne!!)
(437)	2n=16 + 0 n=8	Somenesi, Roumania (ex. Bot. Garden, Cluj) 1965
T.nigricornis (516)	2n=24 +)S, 2S	Amongst irrigated poplars, Bamian, Afghanistan, R.H.S. 1966. (no ref.)

Section Leucantha

T.leucanthum (616	2n= 16 + 0	Wet slopes, 50k. Eof Agri., E. Turkey (1500m), (T.501) P.Crisp, 1-9-1966.

Section Spuria

T.montanum	(546)	2n=40 + 0	Ab Ali Elburz, Iran, R.H.S. 1966 (P.F. 9077)
	(547)	2n=40 + 0	Kapi Dagi Mts., Marmora, Turkey, R.H.S. 1966 (P.F. 8874)
T.syriacum	(617)	2n=48 + 0	Erzincon-Pulumer pass, E-C. Turkey 6000'. P. Crisp, 2-9-1966 (T.226a)

Section Scariosa

T.bithynicum	(621)	2n=16 + 0	25M N.W. Skopje, Yugoslavia, P.Crisp, 17-966 (T.240).

Section Macrocornuta

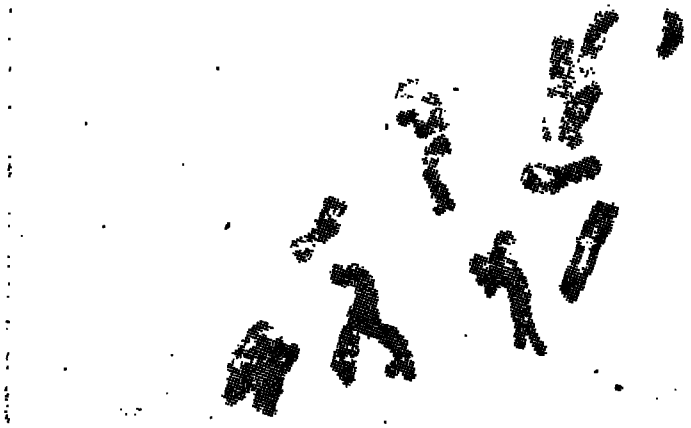
T.kok-saghyz	(90)	2n=32	Ex. Moscow, 1965 (Botanical Garden)
	(93)	2n=24	Ex. 'Switzerland' 1965
	(104)	2n=24	Ex. Bucharest Botanical Garden, 1965
	(125)	2n=25	Ex. Berlin Botanical Garden 1965
T.succulenteum	(186)	2n=32 + 0	Alrout, Morocco, sandy fields, A.P. Hamilton 4-4-1965
T.neo-lobulatum	(510)	2n=24 + 2S	Hajigac Pass, Koh-i-Baba, Afghanistan R.H.S. 1966 (8491)
T.monochlamydemeum	(512)	2n=24+1B	Kishm, Badakstan, Afghanistan, 3000' R.H.S. 1966.
T.wallichii	(515)	2n=16 + 0	Bord-i-Amer, Hinu Kush, Afghanistan, R.H.S. 1966 (P.F. 8416)

Section Kashmirana

T.dentisquameum	(508)	2n=32 + 2S	Hajigac Pass, Koh-i-Baba, Afghanistan R.H.S. 1966 (P.F. 8533)
T.gulmargense	(539)	2n=24 + 2S, 1B	Kashmir, J.L. van Soest, 21-7-1964

Section Eu-Erythrocarpa

T.breviscapum	(511)	2n=24 + 1B	Paghman, 15M N.W. Kabul, Afghanistan, 8200', R.H.S. 1966
T.pseudocalocephalum	(514)	2n=32+0S	Hajigac Pass, Koh-i-Baba, Afghanistan, R.H.S. 1966
T.fedtschenkoi	(517)	2n=24+ 0-1S	Paghman, 15M NW Kabul, Afghanistan, 8000', R.H. S. 1966



Photograph 39. A root-tip squash of an Asian diploid species, T.wallichii, 2n=16. Notice the two large chromosomes shared by many of the primitive sections, possibly due to a translocation.

Section Ceratophora

T.cornutum (428)	2n=24 + 3S	Opdal, Norway, Ex. Bot. Gard. Uppsala, Sweden, 1965
(599)	2n=24 + 0-1S	'Ex Uppsala' (definitely not from Gotland as stated) 1966
T.bicorne (534)	2n=24 + 2S	Ex Bot. Gard. Leiden (J.L.van Soest misit), 1966, Origin unknown

Section Fontana

T.fontanum (89)	2n=24	Ex. Bot. Gard. Moscow, 1964
T.viride (136)	2n=16	Below the Jungfrau, Mrs. S. Dunbar, 5-6-1965
T.viride (137)	2n=18	"

Section Palustria

T.austriniforme (Wicken 1)	2n=32	Wicken Fen, Cambs., as root. S.M. Walters, 1966
T.austrinum (483)	2n=23 + 1B	Cicuta Fen, S. Guernsey, C.I. 23-4-66 A.J.R.
T.balticum (597)	2n=32 + 0	Uppsala, Sweden (ex Bot. Gard. Uppsala 1966)
T.crocodes (433)	2n=40 + 0	Lyl, Sweden (ex Bot. Gard. Uppsala 1966)
T.egregrium (430)	2n=32 + 4S	Öland, Sweden (ex Uppsala Bot. Gard. 1966)
(595)	2n=32 + 0	Gotland, Sweden "
T.limnanthes (602)	2n=40 + 0	" " "
T.murbeckianum (518)	2n=32 + 2S	Hajigac Pass, Koh-i-Baba, Afghanistan R.H.S. 1966

Section Spectabilia

T.akranesense (551)	2n=32 + 0,2S; 0, 1B	20M from U.S. base, Keflavik, Iceland Commander M.Stocken, 1966
T.caledonicum (500,1)	2n=40 + 0S	Head of Glen Doll on W. side, Clova, Angus, wet mica-schist cliff. 6-1965, A.J.R. (as root) 2300'
T.euryphyllum (193)	2n=32	Meadows by Lawers village, Killin, Perth, 300', 12-6-1965, A.J.R.
(452)	2n=32 + 1S	Roadside, 3M. N. of Invergordon, W. Ross, 3-6-1965, A.J.R.
(490)	2n=32 + 1S	Meadow, Staffin, Skye, 50', 4-6-1965 A.J.R.

Section Spectabilia (con.)

T.faeroense	(195)	2n=40 + 0	Flush, Wynch Bridge, Upper Teesdale, N.Yorks. 14-5-1965, A.J.R.
	(197)	2n=40 + 0	"
	(407)	2n=40	Base-rich flush, Sunbiggin Tarn, Crosby Ravensworth, Westmorland. 18-6-1965, A.J.R.
	(408)	2n=40 + 0	"
T.firmum	(410)	2n=32	Base-rich river-bank, Langdon Beck, Upper Teesdale, Durham, 16-6-65, A.J R.
T.fulvicarpum	(524)	2n=32 + 4S	Edge of a damp pine-wood, Braemar, Angus. 3-7-1966, A.J.R.
T.hibernicum	(403)	2n=24	Carex rostrata fen with Black-Headed Gull colony, 4M. N.Kirriemuir Angus. 8-6-1965, A.J.R.
	(404)	2n=24	"
T.larssonii	(411)	2n=32	Base-rich river bank, Langdon Beck, Upper Teesdale, Durham 10-6-65 A.J.R.
T.leptolepis	(529)	2n=40 + 0	Wet roadside, Killiecrankie Pass, Perth, 29-6-1966, A.J.R.
T.maculigerum	(401)	2n=32	Limestone cliffs above the Traligil Inchnadamph, Sutherland, 800' 31-5-65, A.J.R.
	(412)	2n=32 + 0	Base-rich river bank, Langdon Beck, Upper Teesdale, Durham, 10-6-65 A.J.R.
	(455)	2n=32	Roadside, 3M, N. of Invergordon, W.Ross, 3=6=66, A.J.R.
	(528)	2n=32 + 0	Roadside, Rannock Station, Perth, 29-6-1966, A.J.R.
T.naevosum	(458)	2n=24 + 0	Roadside, 4M, N. of Blairgowrie, Angus, 8-6-65, A.J.R.
	(583)	2n=24 + 0	Base-rich grassland, Malham, W. York, 5-1966, A.J.R.
	(584)	2n=24 + 0	Montane grassland, Harbottle, Northumberland, 1200', 6-1966, A.J.R.
	(585)	2n=24+2-3S	Limestone clints, under Fraxinus, Colt Park Woor, Ribblesdale, W. Yorks, 5-1966, A.J.R.
T.norstedtii	(454)	2n=48 + 0	Roadside, Invergordon, W. Ross, 3-6-65, A.J.R.
	(465)	2n=48 + 0	Roadside, Aviemore, Aberdeen, 27-5-65 A.J.R.
T.praestans	(406)	2n=32 + 0	Base-rich flushes, Sunbiggin, Crosby Ravensworth, Westmorland, 18-6-1965 A.J.R.

Section Spectabilia (con.)

T.pseudonorstedtii	(200) 2n=32	Base-rich flushes, Sandsyke, Upper Teesdale, Co. Durham, 16-6-1965 A.J.R.
T.pycnostictum	(498) 2n=32 + 4S	Mica-schist cliffs, Caenlochan Glen, Angus, 3100', 6-1965 (as root) A.J.R.
	(499) 2n=32 + 0	"
	(503) 2n=32 + 0	Mica-schist cliffs, Glen Doll, Angus, 2450', 6-1965 (as root) A.J.R.
	(505) 2n=32 + 0	"
	(MNT 1) 2n=32	Mica-schist cliffs, Meall nan Tarmachan Killin, Perth, 2200' (as root) 6-1965 A.J.R.
T.repletum	(Lawers 1) 2n=32 + 0 (as root-tip and tapetal mitosis)	Mica-schist cliffs, Ben Lawers, Killin, Perth, 3200', 6-1965 (as root) A.J.R.
T.shetlandicum	(519) 2n=24 + 1B	Stackpole Warren, Tenby Pembs, 14-6-1966, D.W. Shimwell.
T.solenophorum	(491) 2n=24+ 0-2S, 0=1B	Wet grassland, Staffin, Skye, 3-6-65, A.J.R.
T.spectabile	(190) 2n=40	Roadside, Lawers Village, Killin, Perth, 12-6-1965, A.J.R.
	(191) 2n=40	"
	(199) 2n=40	Base-rich flush, Sandsyke, Upper Teesdale, Durham 16-6-1965, A.J.R.
	(431) 2n=40 + 0	Meraker, Norway, ex. Uppsala, Sweden 1966, A.J.R.
T.unguilobum	(409) 2n=32	Grassy path Strathtummel, Perth, 10-6-1965, A.J.R.
	(442) 2n=32	Dune slacks, Holy Island, Northumberland, 22-6-1965, A.J.R.
	(443) 2n=32 + 0	Roadside, Loch Ness, Inverness, 3-6-1965, A.J.R.
	(450) 2n=32 + 2B	Machair, Achmelvich, Lochinver, Sutherland, 30-5-1965, A.J.R.
	(451) 2n=32	"
	(453) 2n=32	Roadside, Invergordon, W.Ross, 3-6-1965, A.J.R.
	(487) 2n=32+1 -4S	Roadside, Spean Bridge, Inverness, 5-6-1965, A.J.R.
	(487) 2n=32 + 0	Hill Pasture, Alwinton, Northumberland 1100', 6-1966, A.J.R.

Section Erythrosperma

T.argutum	(445) 2n=24 + 0	Long grass in shade, Strathtummel, Perth, 10-6-1965, A.J.R.
T.austriacum	(183) 2n=16	Clinker path, Haverton Hill, Co. Durham, 20-6-1965, M. Hartley.
	(185) 2n=17	Dry limestone grassland, Hlohovec, C.S.S.R., 4-5-1965, Prof. D.H. Valentine
T.brachyglossum	(158) 2n=24	Dry maritime turf, Greatham Creek Seaton Carew, Co. Durham, 4-5-1965, A.J.R.
	(164) 2n=28	"
	(168) 2n=24	"
	(169) 2n=24	"
	(171) 2n=24	"
	(172) 2n=24	"
T.disseminatum	(128) 2n=24 + 0	Ex. Bot. Gard. Berlin, origin unknown, 1965.
T.dissimile	(496) 2n=24 + 3S	Grey dunes, Ynyslas, Cardigan, 8-1965 (as root), Prof. D.H. Valentine
T.isophyllum	(146) 2n=16 + 2S	Dry limestone grassland, Kovacover Kopce,
	(147) 2n=16 + 0S	C.S.S.R. 4-5-1965, Prof. D.H.Valentine
	(148) 2n=16 + 0S	"
	(154) 2n=16	" (Hlohovec)
	(149) 2n=24	"
	(151) 2n=24	" (Hlohovec)
	(152) 2n=24	"
	(153) 2n=24	" (Hlohovec)
	(194) 2n=24	" (S.Slovakia)
	(440) 2n=16, 22	"
	(131) 2n=24	Ex. Bot. Gard. Jasi, Roumania, Origin unknown, 1965.
T.lacistophyllum	(Sherburn Hill 16) 2n=24	Dry limestone grassland, Sherburn Hill, Co. Durham, 6-1966, A.J.R.
T.oxoniense	(111) 2n=32	Grey dunes, Warkworth, Northumberland, 21-5-1965, A.J.R.
T.proximiforme	(178) 2n=24	Wood margin on limestone, Shadforth Dene, Sherburn, Co. Durham, 20-5-1965, Prof. D.H. Valentine
T.pseudolacistophyllum	(45) 2n=32	Grey dunes, Drigg point, Ravenglass, Cumberland, 22-8-1964, A.J.R.
T.rubicundum	(417) 2n=24	Millhaven, Pembroke; 8-1965, Prof. D.H. Valentine.
T.silesiacum	(446) 2n=23, 24 + 0-3S	Grassy path, Strathtummel, Perth, 10-6-1965, A.J.R.

Section Erythrosperma (con.)

T.simile	(494)	2n=32 + 4S	Grey dunes, Ynyslas, Cardigan, 8-1965, Prof. D.H. Valentine. (as root).
T. taeniatum	(586)	2n=24 + 0	Roadside, Tomphubil, Perth, 6-1965, A.J.R.
T.tanylobum	(Brat, 1-3)	2n=24, 26	Dry grassland, Bratislava, C.S.S.R., 5-1965, D. H. Valentine (root)
T.tortilobum	(553)	2n=24 + 1B, 2-3S	Roadside, N.W. Auvergne, France, 22-8-1966, A.J.R.
	(594)	2n=25 + 2S	Baleo, Spain, 6-1966, D.M. John.

Section Boreigena

T.cochleatum	(435)	2n=24 + 2S	Sodankyla, Finland, ex. Bot. Gardn. Uppsala, 1965.
	(605)	2n=24 + 1-2S	ex. Uppsala, Bot. Gard. Sweden 1966; origin unknown.

Section Vulgaria

T.acutangulum	(554)	2n=24 + 2S	Roadside. N.W. Auvergne, France, 22-8-1966, A.J.R.
T.bractaetum	(8)	2n=24	Garden, Science Labs, Durham, 6-10-1964 A.J.R.
	(459)	2n=23, 24+0-2S	Roadside, Blairgowrie, Angus, 8-6-1965, A.J.R.
	(460)	2n=24+0-1S	"
T.cordatum	(480)	2n=24 + 0	Garden, Philadelphia City, U.S.A. (Alien), 4-1966; Dr. J.L.Crosby.
T.crispulum	(167)	2n=24	Long grass by road, Greatham Creek, Seaton Carew, Co. Durham, 4-5-65, A.J.R.
T.cyanolepis	(604)	2n=24 + 0	Uppsala, Sweden, ex. Uppsala Bot. Gard. 1966.
T.dahlstedtii	(119)	2n=27	Sandy path near sea, Seaton Carew, Co. Durham, 7-5-65, A.J.R.
	(456)	2n=24 + 0	Roadside, Bonar Bridge, W. Ross; 3-6-1965, A.J.R.
T.dentilobum	(593)	2n=24 + 0, 3S	Garden, Les Saintes-Maries de la Mer, La Camargue, Provence, France, 8-1966, A.J.R.
T.duplidentifrons	(135)	2n=16,24 (siblings)	Limestone grassland, Hlohovec, C.S.S.R. 1964, Prof. D.H. Valentine.
	(414)	2n=24	Alder Carr, Newham Bog, Seahouses, Northumberland 21-5-65, A.J.R.
	(415)	2n=24	"

Section Vulgaria (con.)

T.hamatum	(13)	2n=24	Garden, Durham City, 4-10-1964, A.J.R.
	(3)	2n=24	Garden, Science Labs. Durham City, 6-10-1964, A.J.R.
	(15)	2n=24	"
	(16)	2n=24	"
	(117)	2n=24	Roadside, Witton Gilbert, Co. Durham 7-5-1965, A.J.R.
	(463)	2n=24+0-1S	Roadside, 4M.E. Dunkeld, Perth, 10-6-1965, A.J.R.
	(482)	2n=24+1-2S, 2B	Water meadows, S. Guernsey, C.I. 23-4-1966, A.J.R.
T.hamiferum	(520)	2n=24 + 2S	Worm's Head, Gower, Glamorgan; 17-6-1966, D.W. Shimwell.
	(489)	2n=24 + 2B	Roadside nr. Pitlochry, Perth, 10-6-1965, A.J.R.
T.klingstedtii	(421)	2n=24+0-1S	Ex. Bot. Gard. Zakopane, Poland as T.nigricans, origin unknown, 1965,
	(448)	2n=24+3S	Meadow at 3800', Zakopane, Poland, 7-1965, A.J.R.
	(449)	2n=22, 24, 25 + 0-2S	"
T.litorale	(142)	2n=24	Zealand, Denmark, 10-6-1965, Mrs. S. Dunbar.
	(143)	2n=25	"
T.microcarpum	(622)	2n=24+0	Skopje, Yugoslavia, 17-9-1966, P. Crisp.
	(625)	2n=24 + 0	50K. N. of Skopje, Yugoslavia, 17-9-1966, P. Crisp.
T.multifidum	(28)	2n=26	Plymouth Harbour, Devon, ?date; ? source.
T.oreinicolum	(623)	2n=24+2-3S	Arona, Italy; 20-9-1966, P. Crisp.
T.polyodon	(81)	2n=25	Garden, Reading, Berkshire, 8-1964. A.J.R.
	(114)	2n=16, 17	Roadside, Sherburn, Co. Durham; 7-5-1965, A.J.R.
	(140)	2n=24	Zealand, Denmark, 10-6-1965, Mrs. S. Dunbar.
	(155)	2n=24	"
	(162)	2n=24	Long grass near sea, Greatham Creek, Co. Durham, 4-5-1965, A.J.R.
	(163)	2n=26	"
T.pseudohamatum	(588)	2n=24 + 0	Garden, Glanton, Alnwick, Northumberland, 8-1965, A.J.R.
T.sellandii	(492)	2n=28	Roadside, 2M.W. of Staindrop, Co. Durham, 5-1965, A.J.R.
T.alatum	(493)	2n=24+0-3S	Roadside, 2M, E. of Staindrop, Co. Durham, 5-1965, A.J.R.

Section Vulgaria (con.)

T.speciosum (141) 2n=24 Sand-dune, Zealand, Denmark, 10-6-65, Mrs. S. Dunbar.

All hybrid counts which I have made are listed in appendix 4. As none of these plants were found wild, but are the result of experimental crosses, they do not have a place in this appendix.

Appendix 4

A SUMMARY OF ALL KNOWN CHROMOSOME COUNTS IN TARAXACUM

Section Rhodotricha		
T.kotschyi	2n=16 + 0	Richards
Section Oligantha		
T.oliganthum	2n=16 + 0	Richards
Section Leucantha		
T.leucanthum	2n=16 + 0	P. Crisp (verb. comm.) Richards
T.albidum	2n=40	Gustafsson 1933
Section Orientalia		
T.stevenii	2n=16 + 0	Richards
Section Leptocephala		
T.bessarabicum	2n=16 + 0	Gustafsson 1935b Poddubnaja-Arnoldi 1939 Richards
T.nigricornis	2n=24 + 0	Richards
Section Serotina		
T.serotinum	2n=16 + 0	Gustafsson 1933 Poddubnaja-Arnoldi 1939 Małecka 1964 Richards
T.haussknechtii	2n=16 + 0	Richards
Section Porphyrantha		
T.porphyranthum	2n=24	Gustafsson 1935b, 1933
Section Spuria		
T.montanum	2n=40 + 0	Poddubnaja-Arnoldi and Dianova, 1934 Richards
T.syriacum	2n=48 + 0	Richards
Section Macrocornuta		
T.multiscaposum	2n=16	Poddubnaja-Arnoldi and Dianova 1934
T.monochlamydeum	2n=16	" " "
T.wallichii	2n=16,24	Hoy-Liu 1963
	16 + 0	Richards

Section Macrocornuata con.		
T.kok-saghyz	2n=16	Poddubnaja-Arnoldi and Dianova 1934
	2n=24,25	Richards (Agricult. material-autoploids?)
T.microspermum	2n=24	Poddubnaja-Arnoldi and Dianova 1934
T.succulenteum	2n=32 + 0	Richards
T.neo-lobulatum	2n=24 + 25	Richards
Section Sinensia		
T.bicolor	2n=24	Erlandsson 1939
T.vepallidum	2n=40	"
Section Kashmirana		
T.elegans	2n=16	Hoy-Liu, 1963
T.fulvo-brunneum	2n=16	"
T.vulpinum	2n=24	"
T.gulmargense	2n=24+2S, 1B	Richards
T.dentisquameum	2n=32 + 0	Richards
Section Tibetana		
T.heybroekii	2n=16	Hoy-Liu, 1963
T.mitalii	2n=24	"
T.sikkimense	2n=40	Erlandsson, 1939
Section Mongolica		
T.platycarpum	2n=16	Gustafsson 1933
	2n=16, 18	Takemoto 1954
T.mongolicum	2n=32	Gustafsson 1933
Section Scariosa		
T.minimum	2n=16	Gustafsson, 1933
T.bithynicum	2n=16 + 0	Richards
T.hybernum	2n=32	Poddubnaja-Arnoldi and Dianova 1934
T.cyprium	2n=32	Haran 1952
T.megalorrhizon	2n=32	Anzalone 1948
Section Rhodocarpa		
T.schroeterianum	2n=32	Gustafsson 1933
	2n=24	Hoy-Liu 1963

Section Eu-Erythrocarpa		
T.amborum	2n=24	Gustafsson 1935b
T.pieninicum	2n=16	Małecka 1961
T.pseudocalocephalum	2n=24 +1B	Richards
T.fedtschenkoi	2n=24 + 0	Richards
T.breviscapum	2n=24 + 1B	Richards
Section Erythrosperma		
T.agaurum	2n=24, 32	Hoy-Liu 1963
T.dunense	2n=24	"
T.taeniatum	2n=24	"
	2n=24 + 0	Richards
T.tortilobum	2n=24	Hoy-Liu 1963
	2n=24 + 1B, 2-3S	Richards
T.fulvum	2n=32	Gustafsson 1935B
T.ruberulum	2n=24	"
T.tenuilobum	2n=24	"
T.dissimile	2n=24	Gustafsson 1935B, Richards
T.parnassicum	2n=24	"
T.lacistophyllum	2n=24	"
	2n=24 + 0-2S	Richards
T.oxoniense	2n=32	Richards
T.disseminatum	2n=24	Richards
T.austriacum	2n=16, 17 + 2S	"
T.isophyllum	2n=16,17,22,23,24,+2S	"
T.brachyglossum	2n=24,25,26,27,28,+0-3S	Richards
T.proximiforme	2n=24	Richards
T.pseudolacistophyllum	2n=32	"
T.argutum	2n=24 + 0S	"
T.silesiacum	2n=23,24, +1,2,3S	"
T.simile	2n=32 + 0S	"
T.friesii	2n=32 + 0S	Richards
T.tanylobum	2n=24, 25, 26	"
Section Obliqua		
T.obliquum	2n=24	Hoy-Liu 1963
	2n=24	Gustafsson 1933

Section Laevia		
T.pumilum	2n=16	Holmen 1952
	2n=16	Jorgensson and Sörensen 1957
	2n=16, 32	Mosquin and Hayley 1966
T.tundricolum	2n=36	Takemoto 1960
T.arcticum	2n=40	Flovik 1940
	2n=40	Holmen 1952
	2n=40	Erlandsson 1939
T.phymatocarpum	2n=24	Holmen 1952
	2n=24	Mosquin and Hayley 1966
	(2n=40)	Erlandsson 1939 (=arcticum?)
Section Ceratophora		
T.alpicola	2n=24	Takemoto 1954
T.macilentum	2n=24	" 1960
T.arctogenum	2n=32	Holmen 1952
	2n=32	Mosquin and Hayley 1966
T.lacerum	2n=40	Jorgensson and Sörensen 1957
T.ecorniculatum	2n=32	Gustafsson 1935B
T.deliciosum	2n=24	"
T.lactucaceum	2n=32	" 1935A
T.simulum	2n=32	"
T.brachyceras	2n=32	" 1933
T.cornutum	2n=24	"
	2n=24 + 3S	Richards
T.bicorne	2n=24	"
Section Alpina		
T.'alpinum'	2n=32	Gustafsson 1935B
Section Fontana		
T.fontanum	2n=32	Gustafsson 1935B
	2n=24	Richards
T.viride	2n=16, 18 + 0-2S	"
Section Palustria		
T.balticum	2n=32	Gustafsson 1935B
	2n=32 + 0	Richards
T.scaturginosum	2n=24	Gustafsson 1935B
T.lanceolatum	2n=32	"

Section Palustria (con.)

T.egregrium	2n=32 + 4S	Richards
T.crocodes	2n=40 + 0	Richards
T.limnanthes	2n=40 + 0	"
T.austrinum	2n=23 + 1B	"
T.austriniforme	2n=32 + 0	"
T.murbeckianum	2n=32 + 2S	"

Section Spectabilia

T.norcstedtii	2n=48	Gustafsson 1935B
	2n=48	Hoy-Liu 1963
	2n=48 + 0	Richards
T.pseudonorstedtii	2n=32 + 0	"
T.caledonicum	2n=40 + 0	"
T.maculigerum	2n=24	Gustafsson 1935B
	2n=32 + 0S	Richards
T.praestans	2n=32 + 0S	"
T.euryphyllum	2n=32 + 0S	"
T.hibernicum	2n=24 + 0S	"
T.naevosum	2n=24 + 0S, 32+0	"
T.naevosiforme	2n=32	Gustafsson 1933
T.unguilobum	2n=32 + 1-4S	Richards
T.shetlandicum	2n=24 + 1B	"
T.cimbricum	2n=25	"
T.fulvicarpum	2n=32 + 4S	"
T.faeroense	2n=40	Harvey and Hawkes 1963
	2n=40 + 0	Richards
T.spectabile	2n=40 + 0	"
T.leptolepis	2n=40 + 0	"
T.firmum	2n=32	"
T.larssonii	2n=32	"
T.solenophorum	2n=24 + 0-1B, 0-2S	"
T.repletum	2n=32	"
T.pycnoschistum	2n=32 + 0	"
T.akranesense	2n=32 + 0-2S, 0-1B	"

Section Spectabilia (con.)		
T.croceum	2n=32	Gustafsson 1935B
Section Obovata		
T.obovatum	2n=48 + 0	Richards
Section Boreigena		
T.macrocentrum	2n=24	Gustafsson 1933
T.cochleatum	2n=24 + 1-2S	Richards
Section Vulgaria		
T.reflexum	2n=24	Poddubnaja-Arnoldi andDianova 1934
T.duplidens	2n=24	Hoy-Liu 1963
	2n=24	Gustafsson 1933
T.helianthum	2n=24	Hoy-Liu 1963
T.rhaeticum	2n=24	"
T.obtusilobum	2n=16	Gustafsson 1937
	2n=16	Sorensen and Gudjonsson 1946
T.melanthoides	2n=24	Gustafsson 1935B
T.litorale	2n=24	"
	2n=24	Richards
T.sublaeticolor	2n=24	Gustafsson 1935B
T.laeticolor	2n=24	"
T.ekmannii	2n=24	"
T.retroflexum	2n=24	"
T.haematopus	2n=24	"
T.interruptum	2n=24	Gustaffson 1933
T.parvuliceps	2n=24	"
T.mimulum	2n=24	"
T.amblycentrum	2n=24	"
T.fasciatum	2n=24	"
T.crispulum	2n=24	Richards
T.multifidum	2n=26	"
T.longisquameum	2n=24	Gustafsson 1933
T.patens	2n=24	"
T.stenoschistum	2n=24	"
T.pectinatiforme	2n=c.20	"

Section Vulgaria (con.)

T.involucratum	2n=24	Gustafsson 1933
T.latissimum	2n=24	"
T.croceiflorum	2n=c.20	"
T.laciniosifrons	2n=19,20,22,23,24,48	Sörensen and Gudjónsson 1946
T.polyodon	2n=21,22,23,24,44,45, 46,47,48	(and Sörenson 1958)
	2n=16,24,17,18,26,27,28,28,33	Richards
T.cordatum	2n=23,24	Sörensen and Gudjónsson 1946
	2n=24	Richards
T.hamatum	2n=24	Sörensen and Gudjónsson 1946
T.subcyanolepis	2n=16,18,20,24,25,26,27,28,29	Richards
T.speciosum	2n=24	Richards
T.bracteatum	2n=23,24,25 + 0-1S	"
T.hamiferum	2n=24 + 2B	Richards
T.alatum	2n=24 +0, 2, 3S	"
T.cyanolepis	2n=24 + 0	"
T.dentilobum	2n=24 + 0, 3S	"
T.pseudohamatum	2n=24 + 0S	"
T.microcarpum	2n=24 + 0S	"
T.oreinicolum	2n=24 + 2-3S	"
T.acutangulum	2n=24 + 2S	"
T.duplidentifrons	2n=24, 16	"
T.sellandii	2n=28	"
T.klingstedtii	2n=22,24,25 + 1-3S	"
T.dahlstedtii	2n=27,24	"

Species Incertae Sedis

T.nutans	2n=16	Poddubnaja-Arnoldi and Dianova 1934
T.robustum	2n=24	"
T.samuelssonii	2n=32	Gustafsson 1935B
T.confertum	2n=16	" 1933
T.nigricans	2n=32	Małecka 1962
	2n=32 + 0	Richards

Hybrids (Female first)

* T.cordatum x T.obtusilobum	2n=17,18,23,30,31	Sörensen 1958
* T.cordatum x T.polyodon	2n=16,17,18,23	"
* T.polyodon x T.hamatum	2n=22,23,24,25,31,33	"
* T.polyodon x T.bracteatum	2n=22,23,24,25,31,39	"
*T.polyodon x T.chloroleucum	2n=22,23,24,25,31,39	"
* T.laciniosifrons x T.cyanolepsis	2n=22,23,24,25,31,39	"
T.viride x T.fontanum	2n=16,17,18 + 0	Richards
T.isophyllum x T.fontanum	2n=17,18,19 + 0	"
T.polyodon x T.litorale	2n=21,23 + 0S, 2S	"
T.isophyllum x T.succulenteum	2n=16,18,19 + 0-2S	"
T.viride x T.succulenteum	2n=18, + 1S, 20+0	"
T.viride x T.polyodon	2n=17, 18 + 0 -1S	"
T.isophyllum x T.cimbricum	2n=16,18,21 + 0-1S	"
T.viride x T.brachyglossum	2n=17, 18,20 + 0-1S	"

Notes:

All my counts are listed more fully, with localities, in appendix 3 of this thesis.

A number followed by S, indicates the number of satellited chromosomes observed. Similarly, B shows the number of supernumerary chromosomes that were seen.

* In the counts given for the papers Sörensen and Gudjónsson 1946, and Sorensen 1958, it should be noted that very few actual counts are given, and these counts are inferred from the text in some cases. They may not all be correct. Some counts are registered in both papers, not just in the one indicated. Similarly, some of the Gustafsson counts are published in more than one paper.

No counts which have not been specified accurately by an acknowledged

Taraxacum expert are included. Thus all Furnkranz's work, and most of Malecka's has not been included. An exception is T.alpinum, this being the only known count in the section, and possibly belonging to a genuine taxon.

There are 172 species in the genus with chromosome counts. These belong to 29 of the 35 sections. I have counted 93 species in 19 sections. Of these 93 counts, 74 have been new.

Appendix 5

REFERENCES

(N.B. For all taxonomic references before 1900, consult von Handel-Mazzetti, 1907, 'Monographie der Gattung Taraxacum'.)

ANZALONE, B. (1949) Osservazione citoembriologische in Taraxacum megalorrhizon. Annali di Botanici 23, 31-41.

BATTAGLIA, E. (1948) Ricerche sulla parameiosis restituzionale nel genere Taraxacum. Caryologia 1, 1-47.

BLAKESLEE, A.F. (1945) Removing some barriers to crossability in plants. Proc. Amer. Phil Soc. 89, 1-53.

BÖCHER, T.W. (1938) Biological distribution types in the Flora of Greenland. Medd. Grønlands 106, 2.

BÖCHER, T.W. (1952) Contributions to the Flora and Geography of Western Greenland II. Medd. Grønlands 147, 9.

BORGVALL, T. (1959) The Taraxacum-Flora of Boluslan. Acta Hort. Gotob. 22, 1, 1-40.

BORGVALL, T. and HAGLUND, G. (1956) The Taraxacum-Flora of the Gothenburg region. Act. Hort. Gotob. 21, 1, 1-57.

BRENNER, M. (1906) Varietates novae Taraxaci officinalis. Medd. Soc. Fauna Flora Fennica. 32, 196-9.

BRENNER, M. (1907-9) Ibid., 32, 33, 34, 35. Nya vaxtgeographic data.

CHEL'TSOVA, L. (1959) Cell-division during regeneration in the Dandelion root. Dokl. Akad. Novsk. S.S.S.R., Bot. Sci. Sect. 127, 190-7.

CHRISTIANSEN, M.P. (1936) Nye Taraxacum-Arter af Gruppen Vulgaria Dansk. Bot. Ark. 9, 2, 1-57.

CHRISTIANSEN, M.P. (1942) The Taraxacum-Flora of Iceland. Botany of Iceland 3, 3, 236-343.

CHRISTIANSEN, M.P. and WIINSTEDT, K. (1934) Taraxacum, in Raunkiaer C, Dansk Ekskursions-Flora. Copenhagen.

CHRISTIANSEN, M.P. (1942) — En seksuel Maekelbotte-Art fra Schweiz. Nathurhist. Tidende. 6 aarg, Copenhagen.

COOPER, D.C. and BRINK, R.A. (1949) — The endosperm-embryo relationship in a autonomous apomict Taraxacum officinale Bot. Gazette 11, 139-153.

DAHLSTEDT, H. (1900) — Taraxacum, in Andersson and Hesselmann, Bidrag till kännedomen om Spetbergens ach Beerens Islands Kärlväxtflora. Bihang till Kungl. Sv.Vet.Hand, 26, 3.

DAHLSTEDT, H. (1905a) — Om Skandinavska Taraxacum-former. Bot. Notiser, 58, 145-172.

DAHLSTEDT, H. (1905b) — Studier ofver arktiska Taraxaca. Ark. f. Bot. 4, 8, 1-41.

DAHLSTEDT, H. (1906a) — Einiger wildwachsende Taraxaca aus dem Botanische Garten zu Uppsala. Bot. Stud.t. Kjellmann, 164-183. Uppsala.

DAHLSTEDT, H. (1906b) — Artiska och alpina arter inom formgruppen Taraxacum cerathoporum. Ark. f. Bot. 5, 9, 1-44.

DAHLSTEDT, H. (1907a) — Uber einiger im Bergianische Garten kultivierten Taraxaca. Acta Hort. Bergiani 4, 2, 1-31.

DAHLSTEDT, H. (1907b) — Taraxacum palustre und verwandte Arten in Skandinavien. Ark. f. Bot. 7, 6, 1-29.

DAHLSTEDT, H. (1907c) — Taraxacum reichenbachii ssp dovrense. Ark.f. bot. 7, 1, 1-11.

DAHLSTEDT, H. (1907d) — Ueber einiger Sudamerikanische Taraxaca. Ark. f. Bot. 6, 12, 1-19.

DAHLSTEDT, H. (1908) — Taraxacum, in Ostenfeld C.H., Additions and corrections to the Botany of the Faeroes, 3. Copenhagen.

DAHLSTEDT, H. (1909) — Nya Skandinavska Taraxacum-arten. Bot. Notiser, 62, 167-179.

DAHLSTEDT, H. (1910a) — Taraxacum, in Ostenfeld C.H., Christiania videnskselsk skr. 8, 72-79.

DAHLSTEDT, H. (1910b) — Östsvenska Taraxaca. Ark. f. Bot. 9, 10, 1-35.

DAHLSTEDT, H. (1911a) Nya Östsvenska Taraxaca, 10, 6

DAHLSTEDT, H. (1911b) Västsvenska Taraxaca, Ark. f. Bot. 10, 11, 1-79.

DAHLSTEDT, H. (1912) Nordsvenska Taraxaca. Ark. f. Bot., 12, 2, 1-112.

DAHLSTEDT, H. (1913) Taraxacum, in Lindman C.A.N., Svensk Fanerogramflora, Stockholm.

DAHLSTEDT, H. (1921a) Taraxacum, in Printz C., The vegetation of the Siberian-Mongolian frontier.

DAHLSTEDT, H. (1921b) De Svenska arterna av släktet Taraxacum, I, II. Acta Fl. Sueciae, 1.

DAHLSTEDT, H. (1923). Taraxaca från Västra Norge, Berg. Mus. Aarb. 6, 1-36.

DAHLSTEDT, H. (1925) Om Ölands Taraxacum-Flora. Ark. f. Bot. 19, 18, 1-19.

DAHLSTEDT, H. (1926a) Taraxaca from Kamtchatka, collected by E. Hulten, 1920-2. Ark. f. Bot. 20a, 1, 1-15.

DAHLSTEDT, H. (1926b) Taraxacum, in Plantae Sinenses, A. Dre Smith Annis 1921-2 lectae, Medd. fr. Göteborgs Bot. Trad. 14, 43-81.

DAHLSTEDT, H. (1927) In Johnston H.H. Scottish Taraxaca, Trans. and Proc. Bot. Soc. Edinburgh, 29, 4.

DAHLSTEDT, H. (1928a) De Svenska arterna av släktet Taraxacum, III-VII. Kungl. Sv.Vet. Akad. Hand. 3, 6, 1-66.

DAHLSTEDT, H. (1929a) Ueber einiger orientalischen Taraxacum-arten. Acta Hort. Bergiani, 9, 1, 1-36.

DAHLSTEDT, H. (1930a) In Hulten E., Additions to the Flora of Alaska and the Yukon, Kungl. Sv. Vet. Akad. Hand. 8, 2, 219-228.

DAHLSTEDT, H. (1930b) De Svenska arterna av släktet Taraxacum. Kungl. Sv. Vet Akad. Hand. 9, 2, 1-97.

DAHLSTEDT, H. (1932) Taraxacum nutans nov. sp., Sv. Bot. Tidskr. 26, 264-265.

DAHLSTEDT, H. (1933a) Bericht Schweiz Bot. Gesells, 42

DAHLSTEDT, H. (1935) Nya Skandinavska Taraxaca. Bot. Notiser, 88, 295-316.

DAHLSTEDT, H. (1919, 20, 26c, 28b, 29b, 33b) In Druce G.C. Plant Notes, Rep. Bot. Exchange Club of the B.I., 5, 8, 9, 10.

DAHLSTEDT, H. and BORGVALL, T. (1932) — En ny Taraxacum-art av gruppen Erythrosperma. Bot. Notiser 85, 63-66.

DIELS (1922) — Taraxacum platypecidum, in Feddes Repert, 12, 515.

EKSTAM, O. (1897) — Einiger bluthenbiologische beobachtungen auf Spetsbergen. Trömso Mus. Aarsh. 20.

EKLUND, O. (1934) — Studien über die Gattung Taraxacum in Sud-west Finland. Mem. Soc. F. et Fl. Fenn. 10, 137-201.

ERLANDSSON, S. (1939) — The chromosome numbers of some Taraxacum species. Bot. Notiser, 92,,262-264.

FAGERLIND, F. (1947) — Makrosporogenese und Embryosack-bildung bei agamospermischen Taraxacum-biotypen. Sv. Bot. Tidskr. 41, 365-390.

FERNALD, M.L. (1962) — Taraxacum palustre (Wild) D.C. in America. Rhodora 4, 155-7.

FLORSTROM, B. (1914) — Studier over Taraxacum-Florai Satakunta. Acta Soc. F. et Fl. Fenn., 39, 1-124.

FLÖVIK, K. (1940) — Chromosome numbers and polyploidy within the Flora of Spitzbergen. Hereditas, 26, 430.

FRIES, T.C.E. (1908) — Tva nya Taraxacum-arter af Ceratophora-gruppen. Sv. Bot. Tidskr., 3, 2, 1-11.

FÜRNKRANZ, D. (1960) — Cytogenetische Untersuchungen an Taraxacum im Raume von Wien. Österr. Bot. Z., 107, 310-350.

FÜRNKRANZ, D. (1961) — Cytogenetische Untersuchungen an Taraxacum im Raume von Wien. II, Hybriden zwischen T.officinale und T. palustre. Österr. Bot. Z. 108, 408-415.

FÜRNKRANZ, D. (1964) — Cytologische Untersuchungen über experimenteller und naturlich hybriden bei Taraxacum. Berichte Deutsche Bot. Gesells., 78, 3, 139-142.

FÜRNKRANZ, D. (1966) — Untersuchungen an Populatione des Taraxacum-officinale -Komplexes in Kontakgebiet der diploiden und polyploiden Biotypen. Öst. Bot. Zeit, 113, 427-447.

GREENE, (1901) — The North American Taraxaca, Pittonia, 4.

GRIFFITHS, T. (1924) — A note on the periodicity of leaf-form in Taraxacum officinale. Wigg. New Phytologist, 23, 154.

GUSTAFSSON, A. (1932a) Zytologische und experimenteller studien in der Gattung Taraxacum. Hereditas, 16, 41

GUSTAFSSON, A. (1932b) Spontane Chromosomenzahlerhohung in pollenmutterzellen und die denist verbunde Geminibildung. Hereditas, 17, 100

GUSTAFSSON, A. (1933) Über die Teilung der Embryomutterzelle bei Taraxacum. Bot. Notiser 86, 531.

GUSTAFSSON, A. (1934) Die Formenbildung der Totalapomikiten. Hereditas 19, 259-283.

GUSTAFSSON, A. (1935a) Primary and secondary association in Taraxacum. Hereditas, 20, 1-31.

GUSTAFSSON, A. (1935b) Studies on the mechanism of Parthenogenesis. Hereditas 21, 1-111.

GUSTAFSSON, A. (1937a) The occurrence of a sexual population within the apomictic Taraxacum vulgare group. Bot. Notiser, 90, 332

GUSTAFSSON, A. (1947) Apomixis in higher plants. I-III, Act Univ. Lund 42, 3, 43, 2, 12.

HAGLUND, G. (1933). In Samuelsson G. Conspectus ad Floram Graecam. Ark. f. Bot. 26a, 5, 24-27.

HAGLUND, G. (1934) Några nya eller i Sverige nyfunna Taraxacum-arter. Bot. Notiser, 87, 1-41.

HAGLUND, G. (1935a) Some Taraxacum species from Ireland and Wales, cultivated in the Botanica Garden of Lund. Bot. Notiser 88, 429-438.

HAGLUND, G. (1935b) Taraxaca från södra och mellerstra Sverige samt Danmark. Ark. f. Bot. 26, 25-26.

HAGLUND, G. (1936) Några Taraxaca humidsakligen från västra Sverige, Medd. Göteb. Bot. Trä. 11, 39-41.

HAGLUND, G. (1937a) Taraxacum. In Hultén E., Flora of the Aleutian Islands, 337. Oslo.

HAGLUND, G. (1937b) Bidrag till kännedomen om Skandinavians Taraxacum-Flora. I. Bot. Notiser, 90, 445-462.

HAGLUND, G. (1938a) In Steffen H., Nachtrage zur Flora von Nowaja Semlija, eih. Bot. Centralbl. 58b, 105.

HAGLUND, G. (1938b) Taraxacum. In Persson C., A list of flowering plants from East Turkestan and Kashmir . Bot. Notiser 91, 307-317.

HAGLUND, G. (1938c) Bidrag till kännedomen om Skandinaviens Taraxacum Flora II. Bot. Notiser 91, 499-508.

HAGLUND, G. (1941) Taraxacum. In Hylander N., Förteckn. Skandinavien Vaxter 157. Lund.

HAGLUND, G. (1942) Taraxacum, in Holmgren B., Blekinges Flora, Karlshamn.

HAGLUND, G. (1943a) Några nya Taraxaca från Skåne och Danmark. Bot. Notiser, 96.

HAGLUND, G. (1943b) Taraxacum in Arctic Canada. Rhodora, 45, 337-343.

HAGLUND, G. (1946a) Zür Taraxacum-Flora der Insel Öland. Bot. Notiser, 99, 335-363.

HAGLUND, G. (1946b) Contributions to the knowledge of the Taraxacum-Flora of Alaska and Yukon, Sv. Bot. Tidskr., 40, 325-361.

HAGLUND, G. (1948a) Further contributions to the knowledge of the Taraxacum-Flora of Alaska and Yukon. Sv. Bot. Tidskr. 42, 297-336.

HAGLUND, G. (1948b) Contributions to the knowledge of the Taraxacum-Flora of Norway. Nytt Mag. Bot., 86, 45-91.

HAGLUND, G. (1947) Über die Taraxacum-Flora der Insel Rügen. Sv. Bot. Tidskr. 41, 1, 81-103

HAGLUND, G. (1949) Supplementary notes on the Taraxacum-Flora of Alaska and Yukon. Sv. Bot. Tidskr., 43, 1, 109-116.

HAGLUND, G. (1950) Einige Taraxaca aus der Schweiz. Ber.Schweiz Bot. G., 60, 231-243.

HAGLUND, G. (1952) Taraxacum. In Hard av Segerstad F., Den värmlandska kärlväxtsfloras geografi. Göteborgs, K. Sv. Vet et Vitt. Samh., 6b, 362-374.

HAGLUND, G. (1957) Two new Taraxaca from Novaya Zemlaya. Nytt. Mag. Bot., 5, 7-11.

HAGLUND, G. (1963) — Taraxacum in Reichinger K.H., Flora of Syria and the Lebanon, Ark. f. bot., (2), 5, 1, 468-471.

HAGLUND, G. (1941) and LILLIEROTH, G. — Beitrage zur Taraxacum-Flora der Insel-gruppe Lofoten. Nytt. Mag. Naturv 8a, 83-99.

HAGLUND, G. and MORANDER, R. (1937) — Till Hjälmarlandskapens Taraxacum-Flora. Sv. Bot. Tidskr., 31, 3, 339-353.

HANDEL-MAZZETTI, H. von (1905) — Ein neues Taraxacum aus den Westalpen. Osterr. Bot. Z., 55, 461.

HANDEL-MAZZETTI, H. von (1907) — Monographie der Gattung Taraxacum, Leipzig und Wien.

HANDEL-MAZZETTI, H. von (1923) — Nachtrage zur Monographie der Gattung Taraxacum. Osterr. Bot. Z., 72, 254-

HANDEL-MAZZETTI, H. von (1935) — Verh. Zoo. Bot. Ges. Wien, 85, 26-49.

HARAN, N. (1952) — Apomixis in Taraxacum cyprium Lindb. Palestine J.B. 5, 237-247.

HARVEY, M.J. and HAWKES, J.G. (1963) — Marsh Dandelions in Warwickshire. Proc. Birmingham N.H. and Phil. Soc., 20, 2, 14.

HOLMEN, K. (1952) — Cytological studies in the Flora of Peary Land, North Greenland. Medd. om Gronland, 128, 5.

HOY-LIU, S. (1963) — The chromosome numbers of some Taraxacum species. Act. Bot. Neerl., 12, 76-83.

IKENO, S. (1910) — Sind aller Arten der Gattung Taraxacum partheno-genetisch? Ber. Deutsch. Bot. G. 20, 393-397.

JOKELA, P.S. (1963) — Index Taraxacum in the Oulu Herbarium. Aquilo, Ser, Bot., 1.

JUEL, H.O. (1904) — Die Tetradenteilung in der Samenenlage von Taraxacum. Ark. f. Bot., 2, 4, 1-9.

JUEL, H.O. (1905) — Die Tetradenteilung bei Taraxacum und andere Cichorieen. K.Sv. Vet. Akad. Hand., 39, 1-21.

KAPPERT, H. (1954) — Morphology in Taraxacum. Ber. Deutsch. Bot, G. 67, 325.

KEIL, G. (1940) — Das Wurzelwerk von Taraxacum officinale.

KITAGAWA, N. (1933) In Tokyo Bot. Mag., 47, 831.

KITAGAWA, N. (1938) In Rep. Inst. Sci. Res. Manch. 2, 303.

KITAMURA, S. (1933) In Acta Phytotax. et Geobot., 2, 180-221.

KITAMURA, S. (1934) In Acta Phytotax. et Geobot., 3.

KITAMURA, S. (1942) In Acta Phytotax, et Geobot., 11, 276.

KITAMURA, S. (1957) In Mem. Coll. Sci. Univ. Kyoto, B, 24, 1, 14-30

KOIDZUMI, H. (1924) In Tokyo Bot. Mag., 38, 94.

KOIDZUMI, H. (1930) In Kyozai-Koza, 6, 40.

KOIDZUMI, H. (1933) In Journ. Jap. Bot., 9, 360.

KOIDZUMI, H. (1934) In Bot. Mag. Tokyo, 48, 592.

KOIDZUMI, H. (1936) In Journ. Jap. Bot. 12, 618.

KROTOV, G. (1945) A review of literature of Taraxacum kok-saghyz. Rodin. Bot. Review, 11, 417-461. (This review contains all references on, and summarises the work contained in, an extensive body of Russian literature on this important rubber plant.)

KOROLEVA, V. (1939) Interspecific hybridisation in the genus Taraxacum. Compt. Red. Acad. Sci. U.R.S.S., 24, 174-176.

LANGE, T. (1938) Jämtlands Kärlväxtsflora in Act. Bot. Fenn. 21.

LID, J. (1944) List of Taraxacum species in Norway, in Norsk Flora, Oslo.

LINDBERG, H. (1908) Finska Taraxacum-Former. Medd. Soc. F. et Fl. Fenn., 35, 13-30.

LINDBERG, H. (1909) Taraxacum-Former från södra och mellerstra Finland. Acta Soc. F. et Fl. Fenn., 29, 9, 1-48. (Descriptions in Swedish).

LINDBERG, H. (1932) Itinera Mediterranea, Act. Soc. Sci. Fenn. 2, 170-174.

LINDBERG, H. (1935) Die Früchte der Taraxacum-Arten Finnlands. Act. Bot. Fenn., 17, 1-22.

LINDBERG, H. (1944) Taraxacum in Sched. Pl. Finn. Exsicc. Mus. Bot. Helsingforg; Distrib., 21-42, 118.

LUNDBERG, H. (1946) Iter Cyprium. Act. Soc. Sci. Fenn., B,2, 7

MAŁECKA, J. (1958) Chromosome numbers in some Taraxacum-species in Poland, Act. Biol. Crac., 1, 55-56.

MAŁECKA, J. (1961) Studies in the mode of reproduction of the diploid endemic species Taraxacum pieninicum Pawl., Act. Biol. Crac., 4, 25-42.

MAŁECKA, J. (1962) Cytological studies in the genus Taraxacum, Act. Biol. Crac., 5, 117-136.

MAŁECKA, J. (1964) Multinucleate pollen grains in Taraxacum serotinum. Act. Biol. Crac., 7, 107-116.

MAŁECKA, J. (1967) Chromosome numbers of 5 Taraxacum-species from Mongolia. Act. Biol. Crac., 10, 73-83.

MALMIO, B. (1953) Pari uutta Taraxacum-laija. Arch. Soc. Zoo. Bot. Fenn. Vanaamo, 8,1.

MAIMIO, B. (1952) Havaintaja Undenkaupinjin sedun. Arch. Soc. Zoo. Bot. Fenn. Vanaamo, 7, 2.

MARKLUND, G. (1911) Några nya Taraxacum-Arter i Karelia nyfunna. Act. Soc. F. et Fl. Fenn., 34, 7, 1-22.

MARKLUND, G. (1915) Taraxacum-Studier i Ladoga-Karelien. Act. Soc. F. Fl. Fenn, 40, 3, 1-32.

MARKLUND, G. (1925) Nya Taraxaca. Act. Soc. F. Fl. Fenn., 55, 5, 1-25.

MARKLUND, G. (1938) Die Taraxacum-Flora Estlands. Act. Bot. Fenn., 23, 1-150.

MARKLUND, G. (1940) Die Taraxacum-Flora Nylands. Act. Bot. Fenn., 26,1-187.

MARKLAND, G. (1964) A new Taraxacum from Australia, Bot. Notiser, 117, 2, 197.

MACOUN, J.M. (1902) Taraxacum in Canada, Ottawa Nat., 15, 276-7.

MIYAKE, K. (1904) Über das Wachstum des Blutenschafter von Taraxacum.

MOSQUIN, T. and HAYLEY, D.E. (1966) — Chromosome numbers and taxonomic problems in Canadian Arctic plants. Can. J. Bot., 44, 9,1213.

MURBECK, S. (1904) — Parthenogenese bei den Gattungen Taraxacum und Hieracium. Bot. Notiser, 57, 285-296.

NAKAI (1915) — In Tokyo Mag. Bot., 29, 11.

NAKAI (1923) — In Fl. Sylv. Kor., 14, 123.

NAKAI (1926) — In Tokyo Mag. Bot. 40, 576.

NEANDER, G. (1939) — In Sv. Bot. Tidskr. 33, 182.

NELSON, A. (1945) — Rocky Mountain Herbarium Studies. Amer. J. Bot., 32, 290.

OSAWA, J. (1913) — Studies on the cytology of some Taraxacum species. Ark. Zellforsch., 10, 450-469.

PALMGREN, A. (1910a) — In Medd. Soc. F. Fl. Fenn., 37, 39-42.

PALMGREN, A. (1910b) — Bidrag till kannedom on Ölands vegetation och Flora. Act. Soc. F. Fl. Fenn., 34, 1, 1-53.

PALMGREN, A. (1910c) — In Act. Soc. F. Fl. Fenn., 34, 5, 1-16.

PAWŁOWSKI, B. (1924) — Bull. Acad. Polon. Sci., 109-112.

PODDUBNAJA-ARNOLDI, V. and DIANOVA, V. (1934) — Eine zytoembryologische untersuchung einiger Arten der Gattung Taraxacum, Planta, 23, 1-46.

PODDUBNAJA-ARNOLDI, V. (1939a) — The development of pollen and embryo sac in interspecific hybrids of Taraxacum. Compt. Rend. Acad. Sci. U.R.S.S. 24, 374-377.

PODDUBNAJA-ARNOLDI, V. (1939b) — Embryogenesis in remote hybridisation in the genus Taraxacum. Compt. Rend. Acad. Sci. U.R.S.S., 24, 382-385.

PORSILD, A.E. (1938) — Flora of Little Diomede Island in the Bering Straight. Trans. Roy. Soc. Canada, 3, 5, 32, 21-38.

RAILONSALA, A. (1949) — In Ann. Soc. Zoo. Bot. Fenn. Vanaamo., 23, 29.

RAILONSALA, A. (1957) — Taraxaca nova I. Arch. Soc. Zoo. Bot. Fenn. Vanaamo, 11, 148-171.

RAILONSALA, A. (1960) Taraxaca nova II Arch. Soc. Zoo. Bot. Fenn. Vanaamo, 14, 28-43.

RAILONSALA, A. (1962) Taraxaca Nova III, Arch. Soc. Zoo. Bot. Fenn. Vanaamo 17, 150-171.

RAILONSALA, A. (1964a) Taraxaca nova IV, Ann. Bot. Fenn., 1, 1, 55-56.

RAILONSALA, A. (1964b) Taraxaca nova V, Ann. Bot. Fenn., 1, 1, 125-145.

RAILONSALA, A. (1954) In Ann. Soc. Zoo. Bot. Fenn. Vanaamo, 9, 1.

RAILONSALA, A. (1955) In Ann. Soc. Zoo, Bot. Fenn. Vanaamo, 9 sup

RAUNKIAER, C. (1903) Kimdannelse uden Befrugtrig has Melkebotte. Dansk. Bot. Tidskr., 25, 2.

RAUNKIAER, C. (1906, 1934, 1942) Dansk Ekskursionsflora. Copenhagen. Ed. 2, 5, 7.

ROSENBERG, O. (1909) Uber die Chromosomzahlen bei Taraxacum und Rosa. Sv. Bot. Tidskr., 3, 150

RYDBERG, P.A. (1901) Taraxacum alaskanum n.sp., Bull. Torr. Bot. Club., 28, 512.

RYDBERG, P.A. (1905) Taraxacum leiospermum n. sp., Bull. Torr. Bot. Club, 32, 137.

RYDBERG, P.A. (1906) Flora of Colorado, 417, New York.

RYDBERG, P.A. (1917) Flora of the Rocky Mountains, 1037-8. New York.

SAARSOO, B. (1946) Om Ombergs Taraxacum-Flora. Sv. Bot. Tidskr., 40, 362-370.

SAARSOO, B. (1947) Beitrage zur Taraxacum-Flora Est. Sv. Bot. Tidskr., 41, 4, 451-468.

SAARSOO, B. (1949) Übersicht über die Taraxacum-Arten des Baltikuns. Aphoreta Tartuensis, 401-407.

SAARSOO, B. (1958a) Taraxacum railonsalae Hagl. et Saars. Sv. Bot. Tidskr., 52, 2, 352-4.

SAARSOO, B. (1958b) Taraxacum lindstroemii Saars. et Hagl. Sv. Bot. Tidskr., 52, 3, 409-11.

SAARSOO, B. (1962a) In Sv. Bot. Tidskr., 56, 1, 156-174.

SAARSOO, B. (1962b) Tre. nya Taraxacum-Arten from Finland. Bot. Notiser, 115, 65-72.

SAARSOO, B. (1963) Nya Taraxaca från Västkusten. Act. Hort. Gotob., 26, 101-115.

SCHISCHKIN, L. (1964) Taraxacum, in Flora U.R.S.S., 29, 405-560. Moscow and Leningrad.
(All references to previous taxonomic work on the genus in Russia are given in this excellent work, and are not duplicated here. The Flora provides a good synopsis of the taxonomy of Russian Taraxaca.

SCHKORBATOW, L. (1912) Parthenogenetische und apogame Entwicklung bei den Blutenpflazen. Entwicklunggeschictlicht Studien an Taraxacum officinale. Trans. Soc. Natur. Univ. Imp. Kharkow, 45, 15-25.

SEARS, P.B. (1917) Amitotic Parthenogenesis in Taraxacum vulgare and Taraxacum laevigatum. Ohio Journ. Sci. 17, 97.

SEARS, P.B. (1922) Variation in Cytology and gross morphology in Taraxacum. Bot. Gazette, 73, 308-326.

SHERFF, E.E. (1920) The North American species of Taraxacum. Bot. Gazette, 70, 329-358.

SKALINSKÁ, M., CZÁPIK, R, PIOTROWICZ, M. (1959) Further studies in the chromosome numbers of Polish Angiosperms. Act. Bot. Soc. Pol., 28, 487-529.

SOEST, J.L. van (1939) In Nederland Kruidk. Arch. 49, 213-237.

SOEST, J.L. van (1948) Sur quelques Taraxaca et Hieracia du Portugal. Agron. Lusitanica, 10, 6-23.

SOEST, J.L. van (1951) Sur quelques Taraxaca du Portugal. De Flora Lusitana Commentarii, 13, 1,5-14.

SOEST, J.L. van (1952) Sur quelques Taraxaca de la province de Santander. Trabaj. de Jard. Bot. Fac. Farm. Santiago, 3,54

SOEST, J.L. van (1954a) Sur quelques Taraxaca d'Espagne. Collectiana Botanica 4, 1, 1-32.

SOEST, J.L. van (1954b) Sur quelques Taraxaca de Galice. Broeteria, 23, 2-3, 139-143.

SOEST, J.L.van (1954c) Taraxacum braun-blanquetti et quelques autres Taraxaca de France. Vegetatio, 5-6, 524-533.

SOEST, J.L. van (1955a) Taraxacum sectio Vulgaria in Nederland I. Act. Bot. Neerlandica, 4, 1, 82-107.

SOEST, J.L. Van (1955b) Nouvelle contribution pour la connaissance des Taraxaca du Portugal. De. Fl. Lusitanica Comment. 10, 94-98.

SOEST, J.L. van (1956a) New Taraxaca from the Netherlands. Act. Bot. Neerlandica, 5, 1, 94-101.

SOEST, J.L. van (1956b) Les Taraxaca de Belgique I, Bull. Jard. Bot. Bruxelles, 26, 211-235.

SOEST, J.L. van (1957a) Contribution a l'etude des Taraxaca de Corse. Act. Bot. Neerlandica, 6, 407-419.

SOEST, J.L. van (1957b) Taraxacum sectio Erythrosperma. Dt. en sectio Obliqua Dt. in Nederland. Act. Bot. Neerlandica, 6, 74-92.

SOEST, J.L. van (1958a) The Phytogeography of Taraxacum with special reference to Europe. Blumea, supp. 4, 60-67.

SOEST, J.L. van (1958) Taraxacum sect Erythrosperma Dt. em. Lindb. in North America. Act. Bot. Neerlandica, 7, 627-628.

SOEST, J.L. van (1959) Alpine species of Taraxacum. Act. Bot. Neerlandica, 8, 77-138.

SOEST, J.L. van (1960) New species of Taraxacum from Asia. Act. Bot. Neerlandica, 9, 302-326.

SOEST, J.L. van (1961a) Quelques nouvelles especes de Taraxacum. Act. Bot. Neerlandica, 10, 280-306.

SOEST, J.L. van (1961b) New species of Taraxacum from the Himalayan region. Bull. B.M. (N.H.) London, 2, 10, 263-273.

SOEST, J.L. van (1961c) Les Taraxaca de Belgique II, Vulgaria. Bull. Jard. Bot. Brixelles, 31, 319-389.

SOEST, J.L. van (1963) Taraxacum species from India, Pakistan and neighbouring countries. Wentia, 10, 1-91.

SOEST, J.L. van (1964) In Bull. Soc. Franc. Echange, Pl. Vasc. 5.

SOEST, J.L. van (1965a) Taraxacum sectio Palustria Dt. Act. Bot. Neerlandica, 14, 1-53.

SOEST, J.L. van (1965b) Flora der Mongolischen Volksrepublic in Fedd. Repert., 70, 1-3, 60-65.

SOEST, J.L. van (1966a) New Taraxacum species from Asia, I. Koninkl. Nederlands Akad. Wetersch., C, 69, 3, 364-388.

SOEST, J.L. van (1966b) New Taraxacum species from Europe, I. Konickl. Nederlands Akad. Wetersch. C, 69, 4, 433-489.

SOEST,JL. van (1966c) A catalogue of Taraxacum sectio Erythrosperma Dt. em Lindb. Public. Rijksherbarium, Leiden. 1-64.

SOEST, J.L. van (1966d) Taraxacum lanjouwii, a new species from Switzerland. Act. Bot. Neerlandica, 15, 34-5.

SOEST, J.L. van (1966e) In Gorteria, 3, 2, 43-47.

SOEST, J.L. van and LAMBINON, J. (1962) Deux Taraxaca nouveaux de Belgique. Lejeunia, 8, 1-3.

SONCK, C.E. (1964) Drei neues Taraxaca aus dem Finnland Act. Soc. F. Fl. Fenn., 77, 3, 1-6.

SORENSEN, T. (1958) Sexual chromosome aberrants in apomictic Taraxaca. Saet. Bot. Tidskr., 54, 1-22.

SORENSEN, T. and GUDJONSSON, G. (1946) Spontaneous chromosome aberrants in apomictic Taraxaca. Kgl. Dansk. Vidensk. Selsk. Biol. Skr. 4, 2, 1-48.

STORK, H.E. (1920) Studies in the genus Taraxacum. Bull. Torr. Bot. Club., 47, 199-210.

TAKEMOTO, T. (1954) Cytological studies on Taraxacum. Jap. Journ. Genetics, 29, 312.

TAKEMOTO, T. (1960) In Bot. Journ. S.S.S.R. 377.

TATEWAKI (1927) In Trans. Sapp. Nat. Hist. Soc., 9, 191.

TATEWAKI and KITAMURA, S. (1934) Taraxacum in Tatewaki and Kobayashi, Contr. Fl. Aleut., 89.

TSCHERMAK-WOESS, E. (1949) Diploides Taraxacum vulgare in Wien und Niederosterreich, Osterr. Bot., Z., 96, 53-61.

WAGENITZ, (1957) In Willdenowia, 3, 2, 221.

WENDELBO, P. (1949) Om slekten Taraxacum i Norge. Blyttia, 7

WENDELBO, P. (1959) Taraxacum gotlandicum, a Pre-Boreal Relic in the Norwegian Flora? Nytt. Mag. Bot., 7, 161-167.

WENDELBO, P. (1964) Taraxacum seksjonen Obliqua i Norge. Blyttia, 22.

WIINSTEDT, K. (1934) (1959) Taraxacum in Raunkiaer, C., Dansk Ekskursionsflor Ed. 5, Ed. 7.

Appendix 6.

In addition to this list of references concerned with Taraxacum, the following books have been of especial benefit to me in this work:

Davis P.H. Heywood V. (1963),'Principles of Angiosperm Taxonomy.'

Gustafsson A. (1946), Apomixis in higher plants'.

Lewis K.R., John B. (1963), 'Chromosome Marker'.

Sokal R.R., Sneath P.H.A. (1963), 'Principles of Numerical Taxonomy'.

Stebbins G.L. (1950), 'Variation and Evolution in Plants'.