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THE BIOSYSTEMATICS OF TARAXACUM

Being a thesis for the degree of

Doctor of Philosophy at the University of Durham


by

Adrian John Richards

(University College)

'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.

<u>Notes on presentation</u>

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 aggre-

gate 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'.

General are not preceded by the definite article. E.G. species: <u>T.norstedtii</u>;

section: the <u>Spectabilia</u>; genus <u>Hieracium.</u>

6.   A <u>Taraxacum</u> 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 |
| Seotina | 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 |
| Fontana. | 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. | Calathium. diam. | Achene colour. | Rostrum. | Pappus |
|---|---|---|---|---|---|---|---|
| Glacialia | Small, Adp. | Many, thin | Linear, erect | 10–15 mm. | Grey | O | Brown |
| Rhodotricha | Medium. Adp. narrow, fleshy | " | " , scarious margined | 15–25 mm. | Brown | Shorter than achene | Pale reddish |
| Oligantha | Medium, leathery, prickly, Adp. | few | 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. | " | " | " |

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Table 2 (cont.)

*Calathium*

| Section | Size, stature | Scape | Exterior bract. | 쁘. 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.)

Ophthium (handwritten)

| Section | Size, stature | Scape | Exterior bract. | . 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. | *Caloftninm* 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
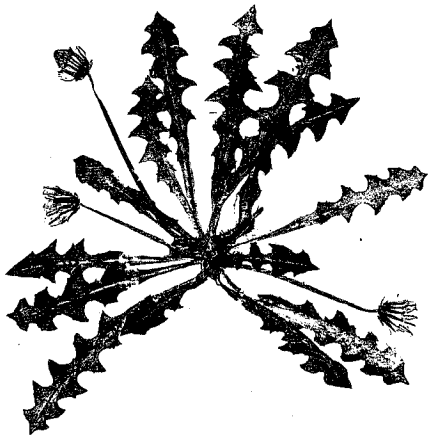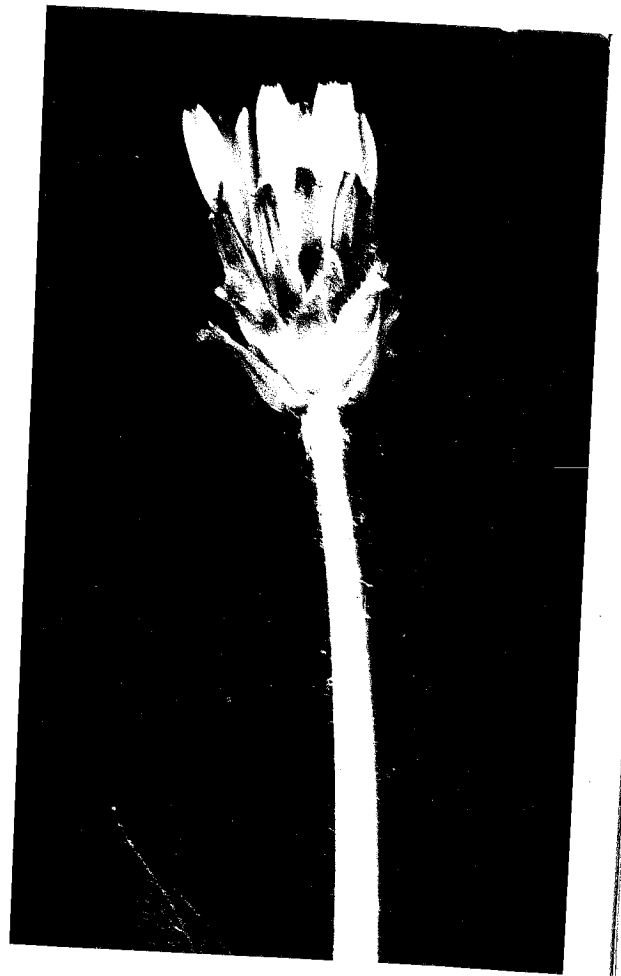
Photograph 1. Herbarium specimen
of Taraxacum kok-saghyz, grown in
cultivation

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, <u>T.kok-saghyz</u> (photo-graph 1) belonging to the <u>Macrocornuta</u>, 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 <u>Vulgaria</u>. A triploid apomict finally resulted (<u>T.kok-saghyz</u> 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. <u>Taraxaca</u> 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 <u>Vulgaria</u> 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, <u>Taraxaca</u> 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~~ achenes

belonging to the section Erythrosperma in an interglacial site containing

the remains of other thermophilous plants, and the discovery of ~~seeds~~ achenes 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

phenonemon 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 Gudjónsson 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 ScandinaviansDahlstedt, 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 particular-
ly 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 bio-
logically 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 Gudjónsson have shown in a remarkable series of experi-
ments (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 <u>Serotina</u> and <u>Leptocephala</u>, which require vernalisation, and the <u>Spectabilis</u>, which rarely flower freely until the second year leaves have been established (except for <u>T. norstedtii</u>).

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 <u>Taraxacum</u> 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 <u>Vulgaria</u>, <u>Spectabilia</u> and <u>Palustria</u> demonstrate virtually identical germination curves, while the <u>Erythrosperma</u> 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 <u>Macrocornuta</u>, 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 <u>Serotina</u> (two species), while the pentaploid <u>Spuria</u> 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.
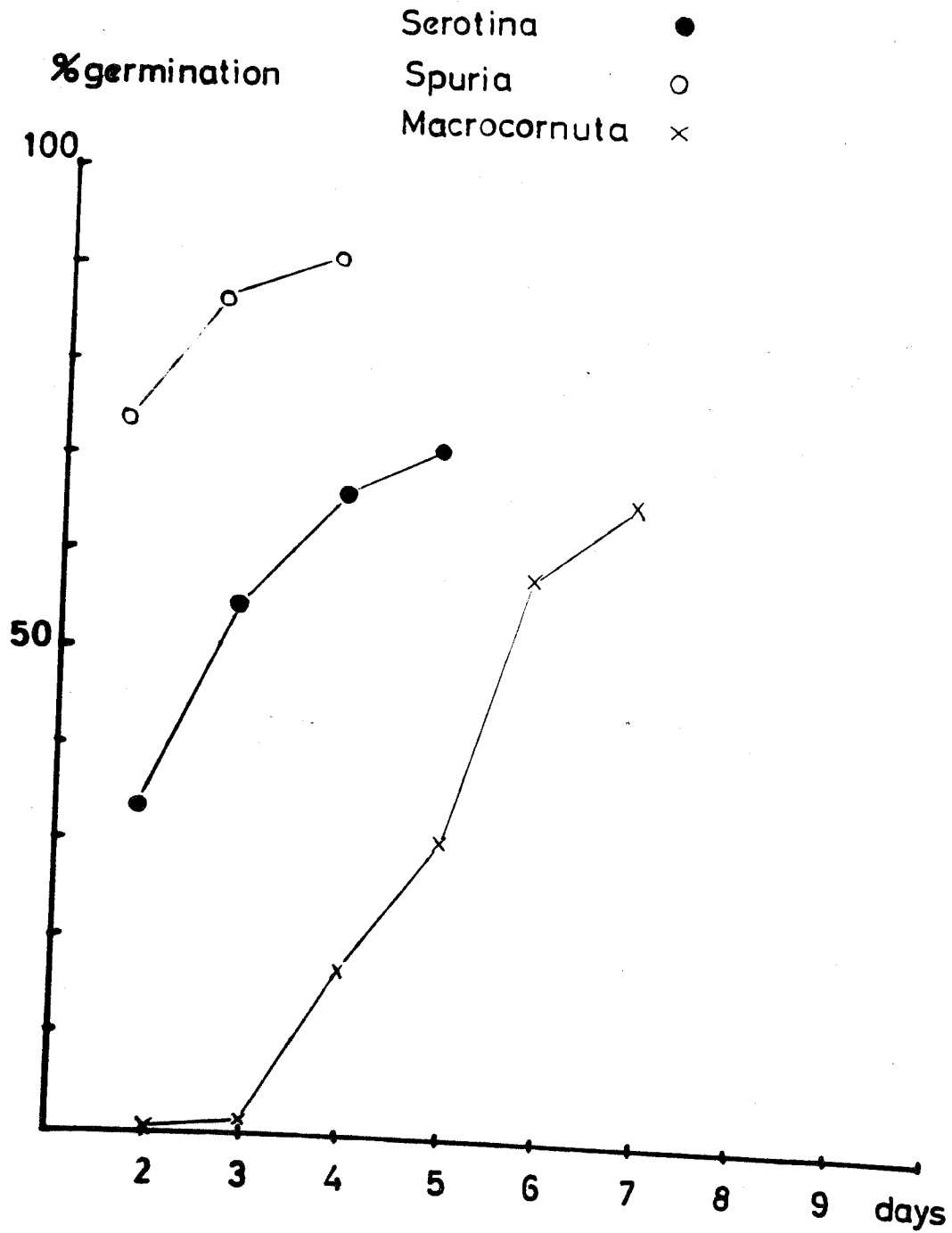
Graph 2. Germination rates of the Serotina, Spuria and Macrocornuta.
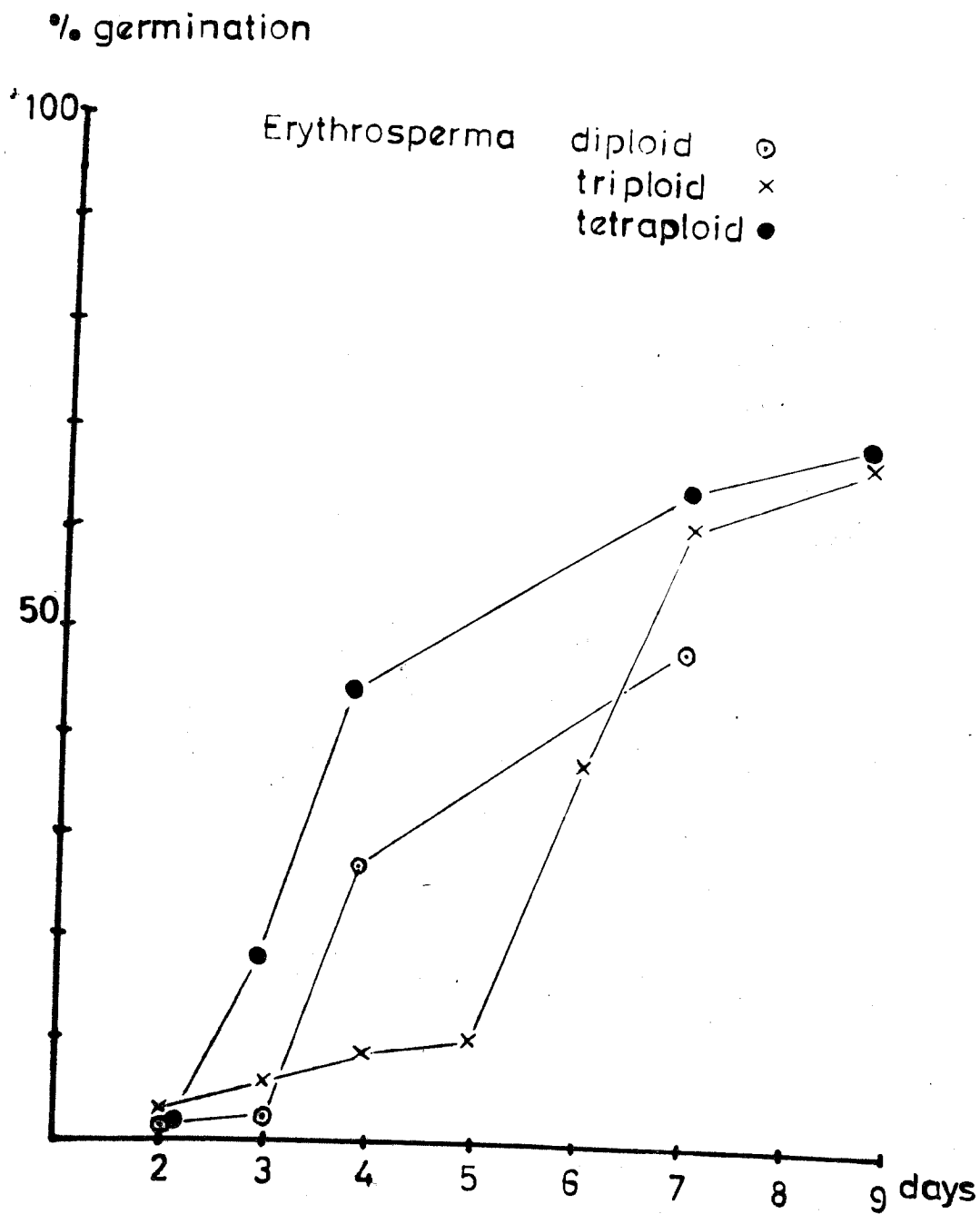
% germination



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

SPECTABILIA LEAF GROWTH

VULGARIA LEAF GROWTH

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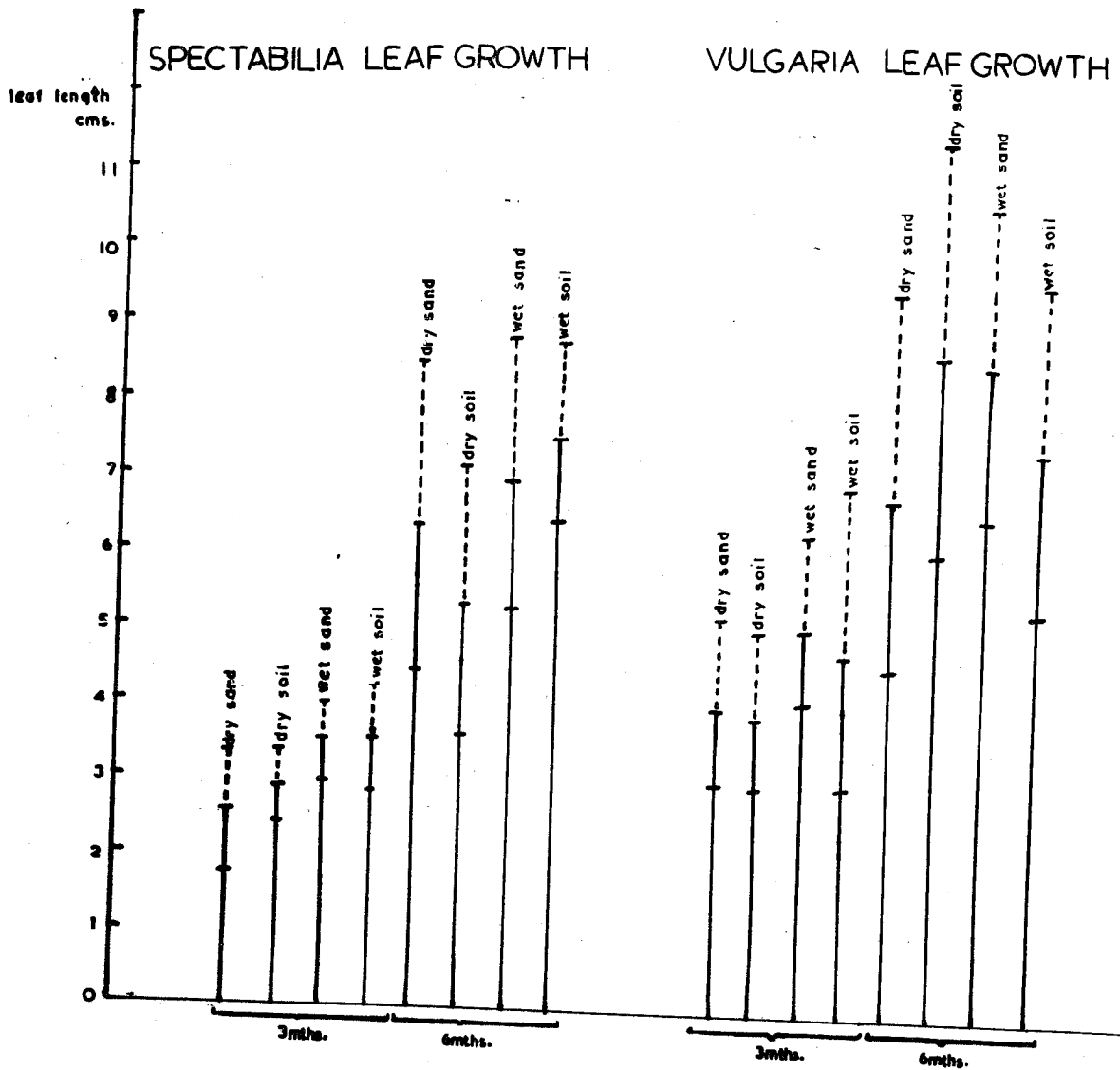
Graph 4. Leaf growth at 3 and 6 months in the Vulgaria and Spectabilia in 4 edaphic regimes, with standard variation shown.

characters by a sample.  This is

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

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 some-
times 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 demons-
trated 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 import-
ance.

## 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 present-
ed 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 |
| | | Dry soil | 8.98mm | 27 | 0.001 |
| | | 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.

## 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 | | O | 2n = 32 |
| T | Fontana | | U | 2n = 40 |
| S | Alpina | | | |
| R | Ceratophora | | L | Dyads 25% + |
| Q | Serotina | | M | Triads 25% + |
| P | Macrocarnuta | | N | Tetrads 60% + |
| O | Others | | | |

Note: "Punch", means cards for O.T.Us possessing this character-state should be punched at the relevant hole.
"Leave" means cards for O.T.Us possessing 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
segregates 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.
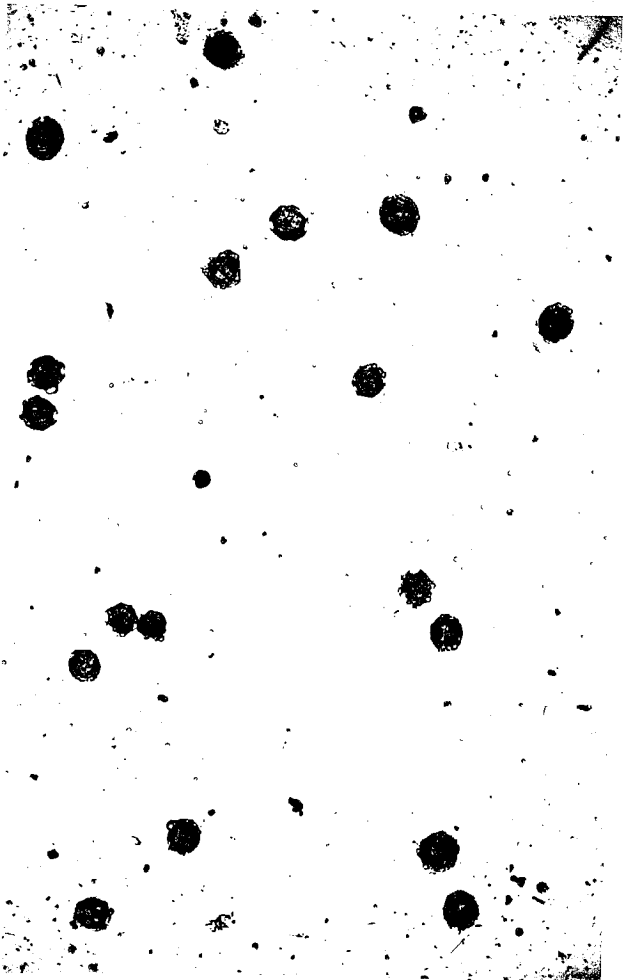
Photograph 21. Regular reductional pollen . T.brachyglossum. Thrislington, Co. Durham.

x 600
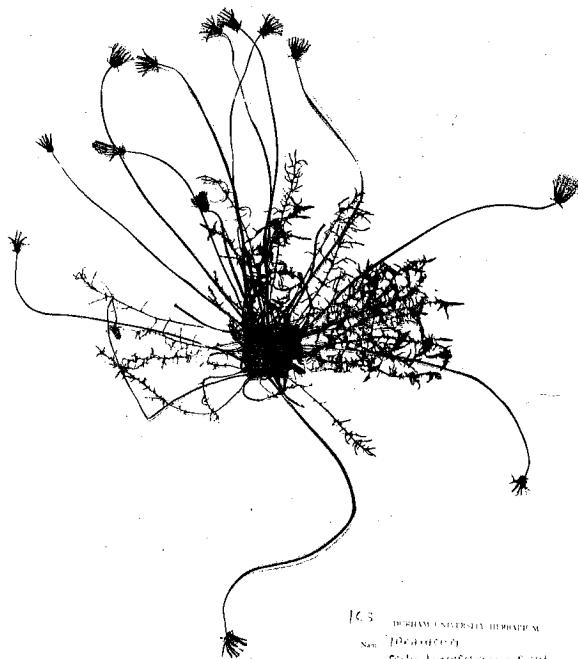
Photograph 22. Herbarium specimen of cultivated T.austriacum; diploid sexual. Haverton Hill, Co. Durham (as an introduction).

x 1/4

Section SPECTABILIA Dahlst

section PALUSTRIA Dahlst

kok‑saghyz
umbrinum
malteanum
pseudonorvegicum
russeolum
norvegicum
tornense
cornutum
hjeltii
perlatescens
hultenii
simulum
lactucaceum
krattlii
platyceras
gallicum

kok‑saghyz
umbrinum
malteanum
pseudo norvegicum
russeolum
norvegicum
tornense
cornutum
hjeltii
perlatescens
hultenii
simulum
lactucaceum
krattlii
platyceras
gallicum

OK SAGHYZ   CANADENSE   CORNUTUM
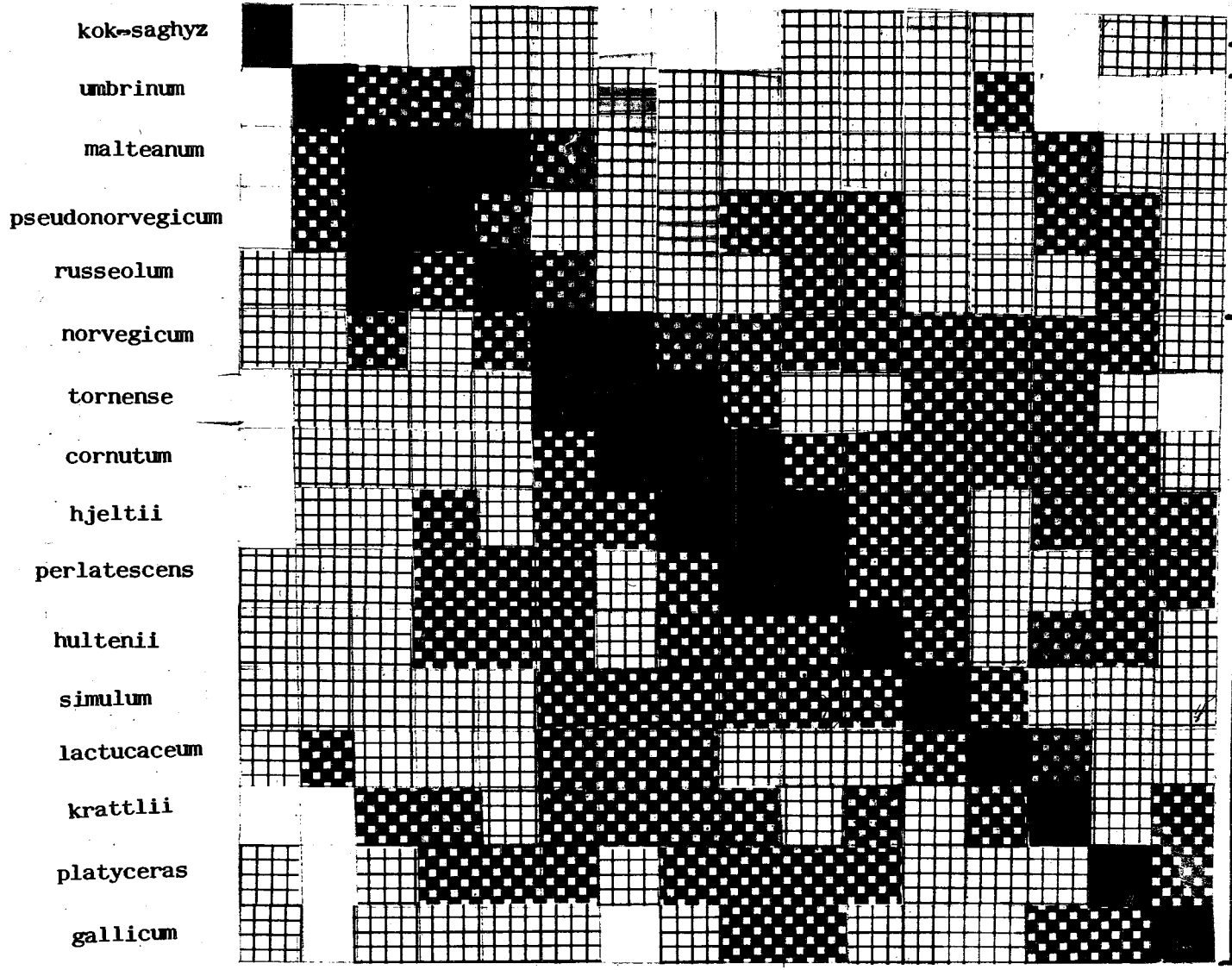
section   CERATOPHORA   Dahlst

Sections CUCULLATA V.S.

FONTANA V.S.

Top axis labels (left to right): graiense, fontanicolum, fontanosquameum, silvicolum, aurantellum, corsicum, peralatum, fontanum, tiriolense, Cucullatum, Caenlochan, Doll, Lawers

Left axis labels (top to bottom): Lawers, Doll, Caenlochan, Cucullatum, tiriolense, fontanum, peralatum, corsicum, aurantellum, silvicolum, fontanosquameum, fontanicolum, graiense

Bottom brackets: FONTANUM, MICACEUM, AESTIVUM CUCULLATUM, GRAIENSE

Row labels (top to bottom):
- rufocarpum
- litanderi
- dissectum
- pacheri
- nevadense
- arcticum
- dourense
- glabrum
- reichenbachii
- handelii
- schroeterianum
- rhodocarpum

Column labels (left to right):
- rufocarpum
- litanderi
- dissectum
- pacheri
- nevadense
- arcticum
- dourense
- glabrum
- reichen bachii
- handelii
- schroet erianum
- rhodo carpum

Bracket labels (right side):
- DISSECTUM
- RUFOCARPUM
- ARCTICUM
- SCHROETERIANUM
- RHODOCARPUM

oreophilum
apenninum
panalpinum
helveticum
corinthaceum
parssenense
pseudofontanum
vernelense
vereinse

oreophilum · apenninum · panalpinum · helveticum · corinthaceum · parssenense · pseudofontanum · vernelense · vereinse

OREOPHILUM ALPINUM

section ALPINA Haglund
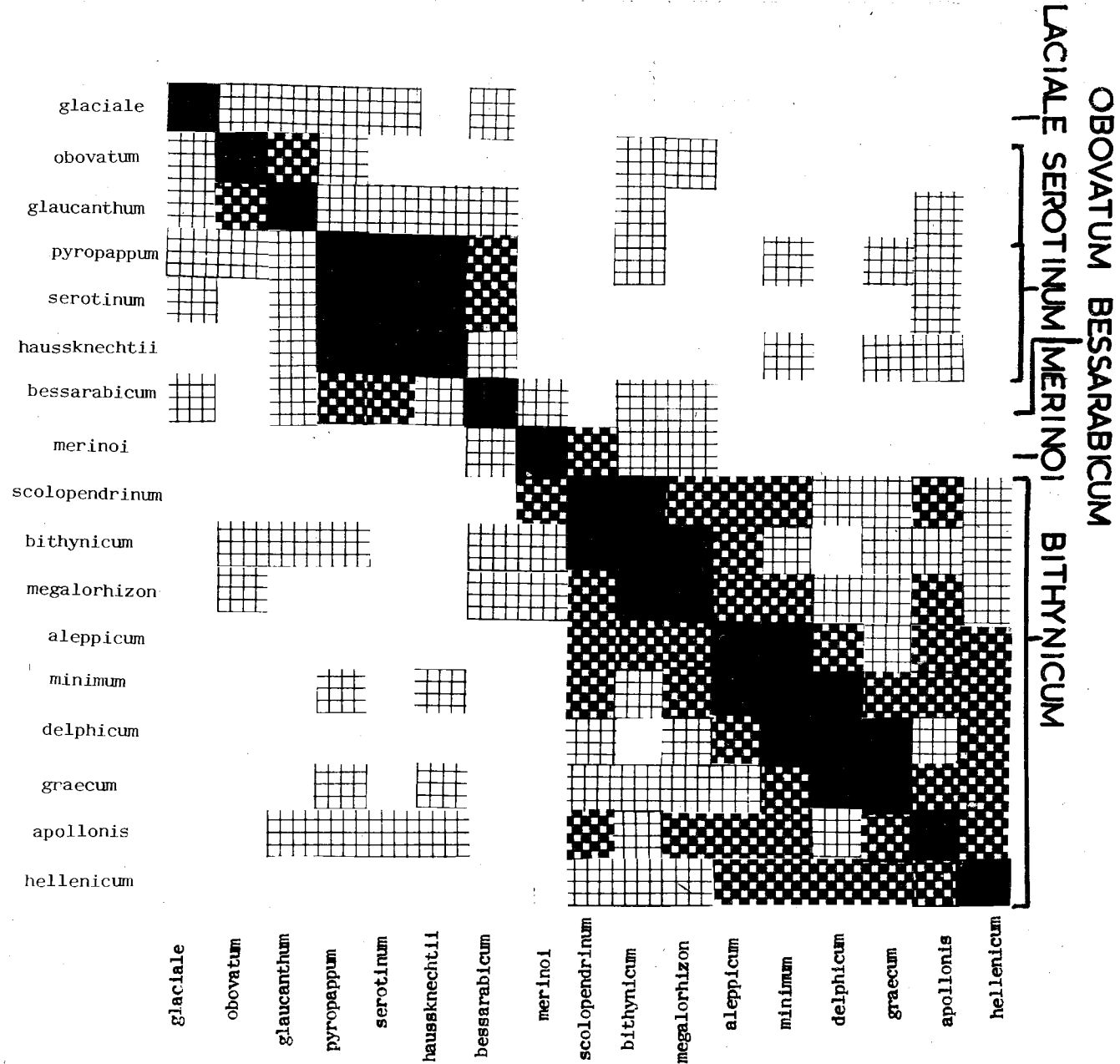
Sections GLACIALIA HM OBOVATA V.S. SEROTINA V.S. LEPTOCEPHALA V.S. SCARIOSA Dahlst

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, Ceratophora, 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 relation-ships lie.  In many cases there were also agreements, and the technique did not appear to be totally without merit, many of its undoubted short-comings 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 non-sense (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 simi-
larity 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 <u>Taraxacum</u> 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 <u>Taraxacum</u> has emerged.

The female meiosis in apomictic <u>Taraxaca</u> 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 repuslion 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
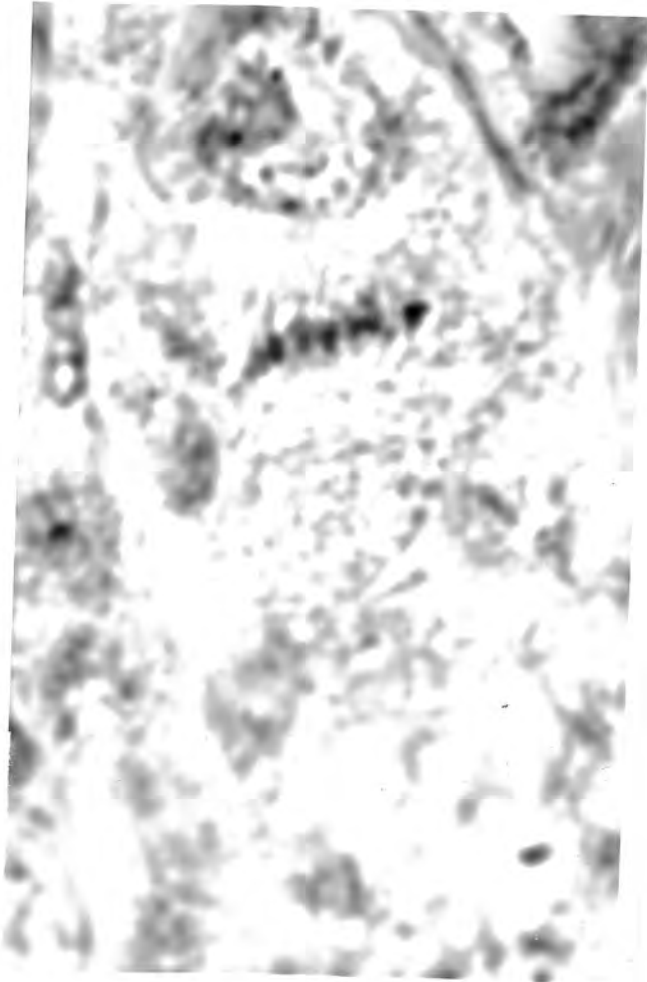
Photograph 6. T.S. of ovule of triploid T.isophyllum, showing a synaptic female meiosis, at metaphase I. Paraffin wax section with Feulgen staining.

x 2000
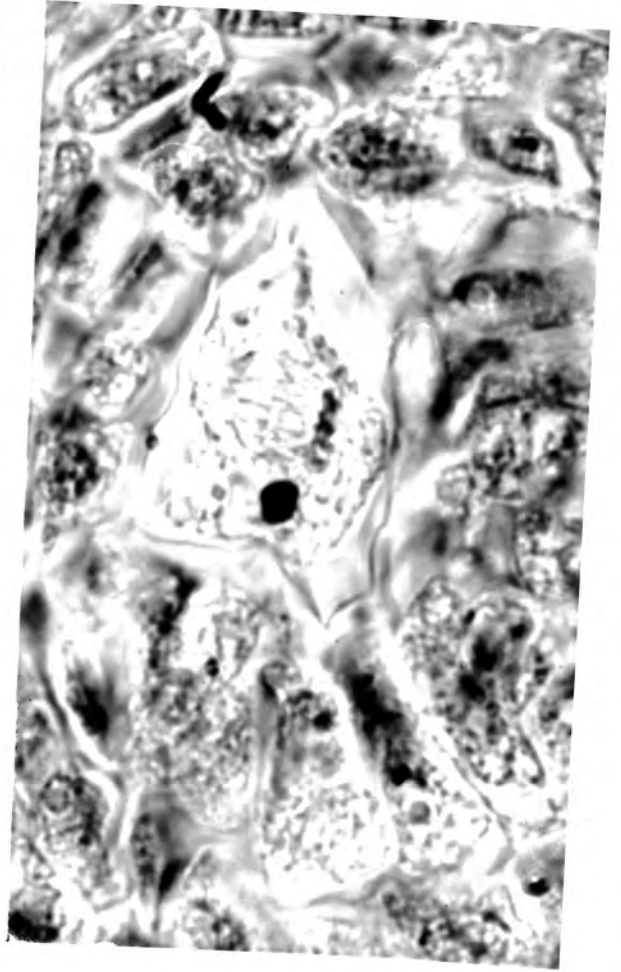


Photograph 7. T.S. of ovule of triploid T.isophyllum, showing a synaptic female meiosis, at anaphase I. Only one pole is in the section, but the spindle is visible. The large black body is an artifact. Paraffin wax section with Feulgen staining.

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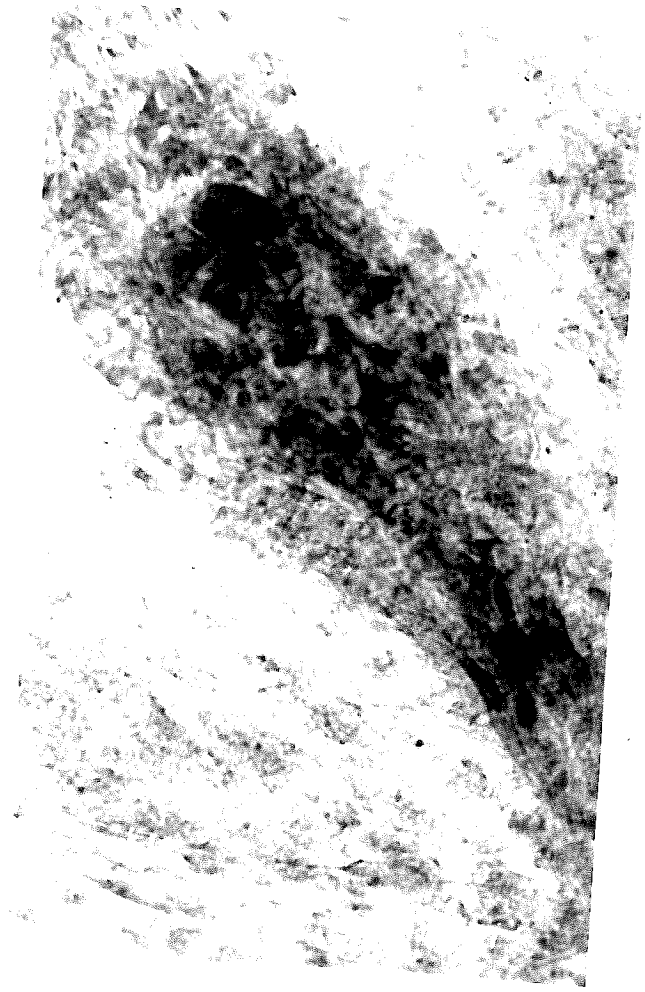
Photograph 9. Embryo-sac of triploid apomictic T. hamatum, showing formation of young embryo (lower right) with un-developed one-cell endosperm (just to the top left of embryo) 24 hours before anthesis. Pectinase dissection technique with Feulgen staining.

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 Gudjónsson (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 Gudjönsson 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.tanylobum 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

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

Photograph 10. Aneuploid *Ttanylobum*, 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 Gudjónsson's plants of this kind.

Sörensen and Gudjónsson (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 Guðjónsson 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 Guðjónsson, 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. Małecka'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.serotinum | 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;

Photograph 11.

T.bessarabicum, section Leptocephala

Ex. Cluj, Roumania, 1966.

Root tip mitosis.



Type 'E', 2. 0u, median,
1, 6, 9, 16 = 4

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

Type 'G' 3, 0u, median,
3, 8, 13, 14 = 4

Type 'I' 4, 0u, median,
4, 7, 10, 11 = 4
                16

Photograph 11.

T.bessarabicum, section Leptocephala

Ex. Cluj, Roumania, 1966.

Root 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
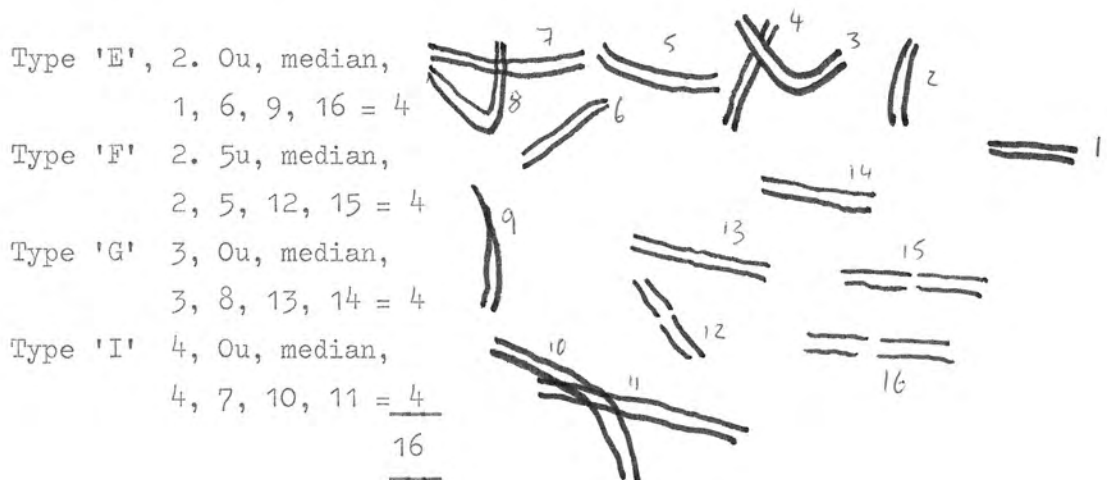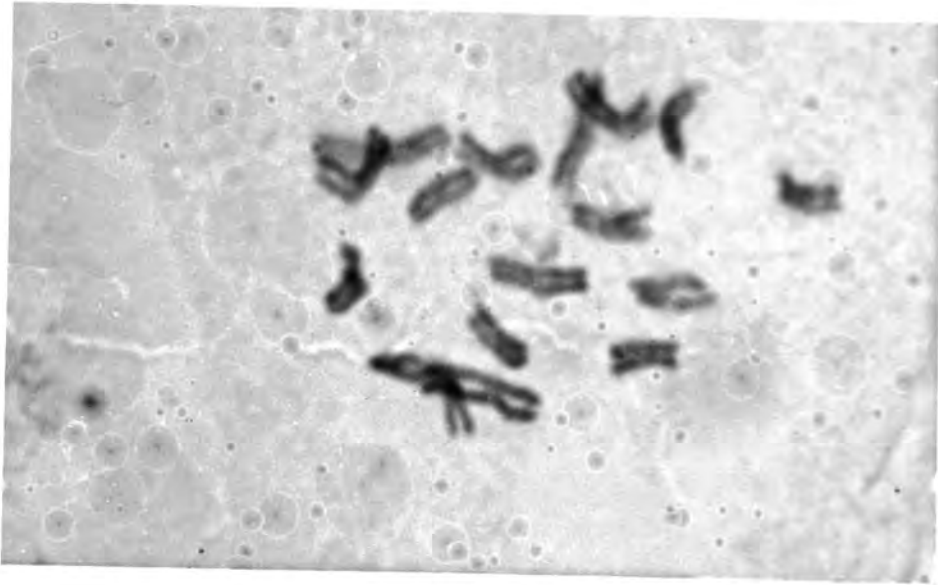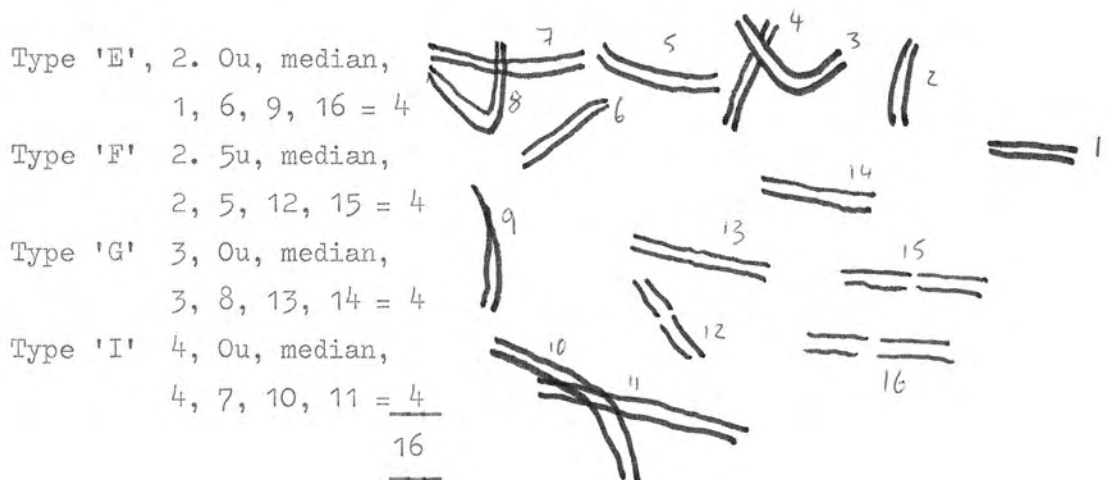
Photograph 12.

T.argutum. Section Erythrosperma.
Ex.Strathtummen, Perth. 6-1965
Root-tip mitosis
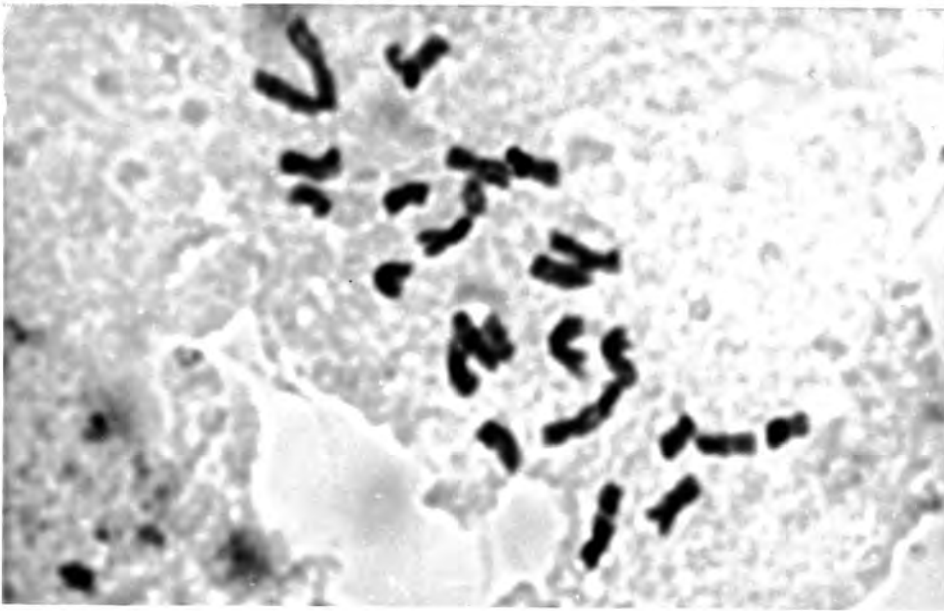


Type 'A', 1.8 u, median,
      2, 4, 6, 8, 9, 11
      13, 14, 16, 18, 19, 23.  = 12

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
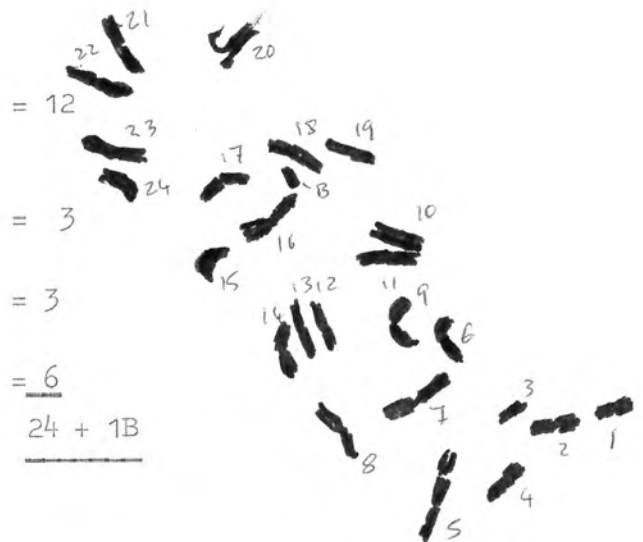
Photograph 13

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 + 2S

Photograph 14

T.larssonii. Section Spectabilia.
Ex. Langdon Beck, Durham, 6-1965
Root-tip mitosis
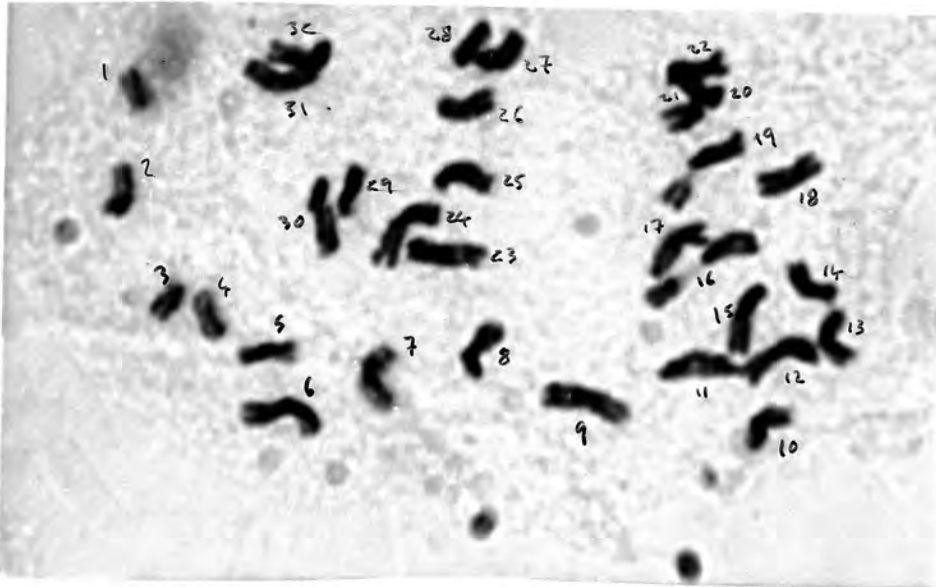


Type 'A' or 'E' 1.8-2 Ou, median

        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

Photograph 15

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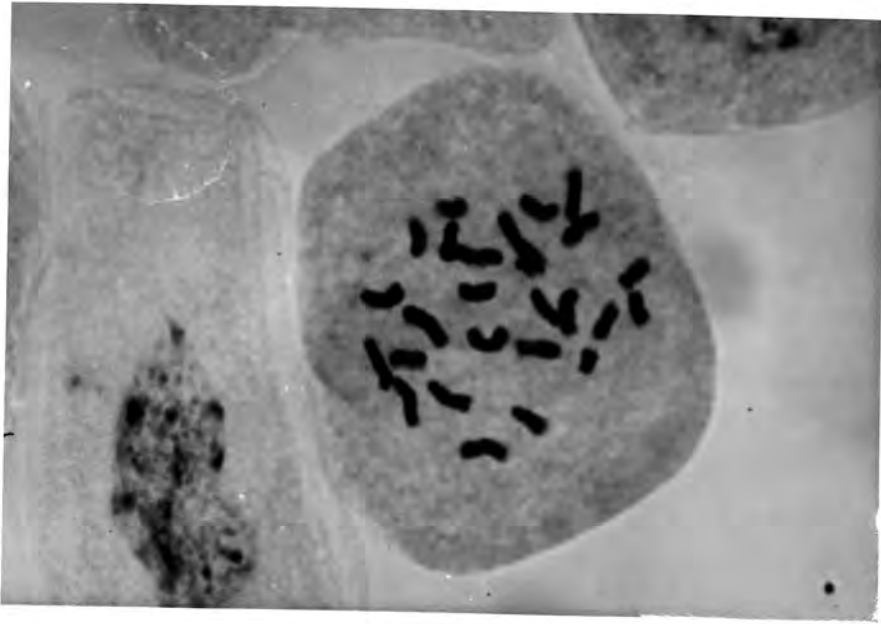


| | | | |
|---|---|---|---|
| Type 'A' | 1.8u, median | | |
| | 1, 9, 11, 15, 22, 24 | = 6 | |
| Type 'B' | 1.6u, median | | |
| | 2, 4, 12, 19, 20, 21 | = 6 | |
| Type 'C' | 2.2u, sub-median | | |
| | 7, 8, 12 | = 3 | |
| Type 'D' | 1.8u + satellite 0.8u | | |
| | 3. 16. 17 | = 3 | |
| Type 'E' | 2.0u,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

Photograph 16

T. hibernicum.  Section Spectabilia.

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

Root-tip mitosis
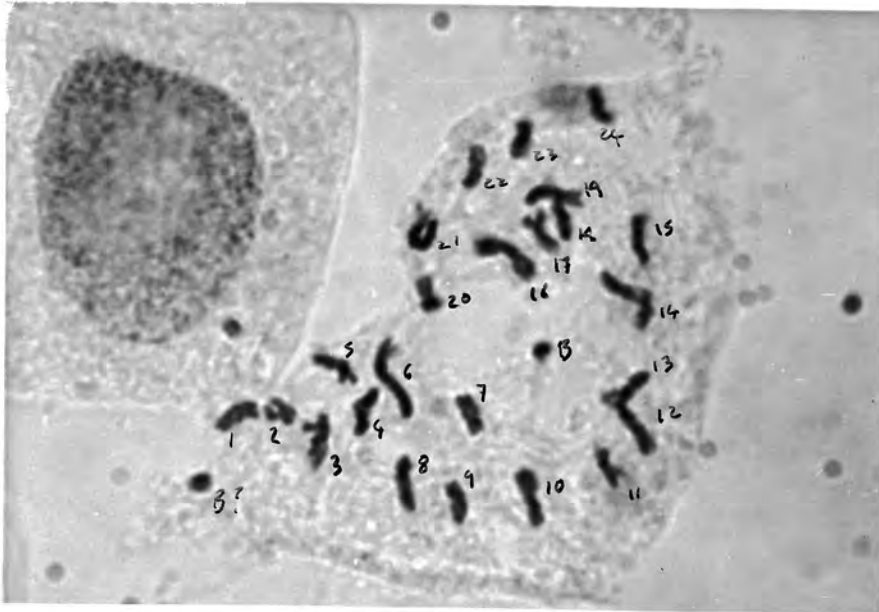


Type 'A'   1.8u, median
           1, 4, 5, 7, 9, 11
           13, 17, 18, 22, 23, 24   = 12

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

Photograph 17

T.serotinum, section Serotina.

Ex.Jasi, Roumania, 1964

Root-tip mitosis
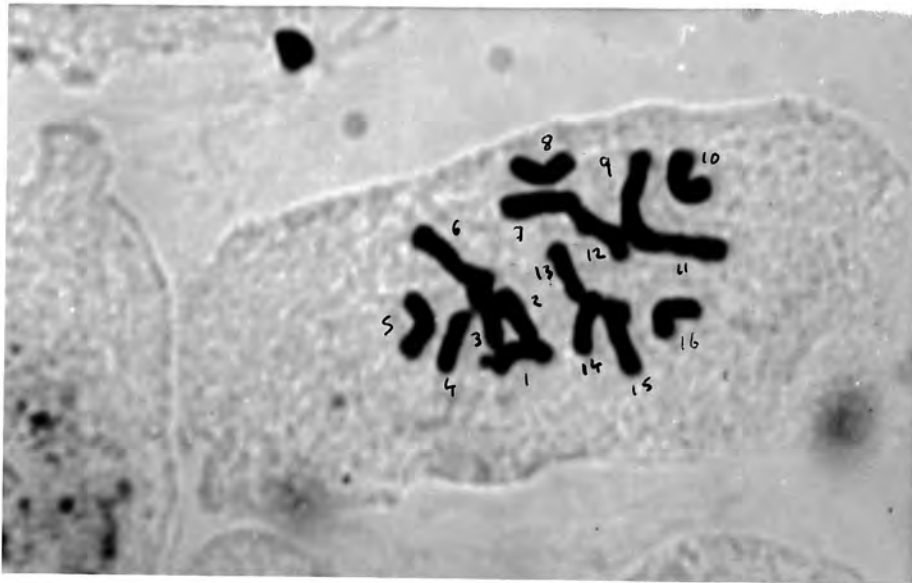


Type 'A' 1.8u, Median
        1, 4, 10, 16    = 4

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
                            ===

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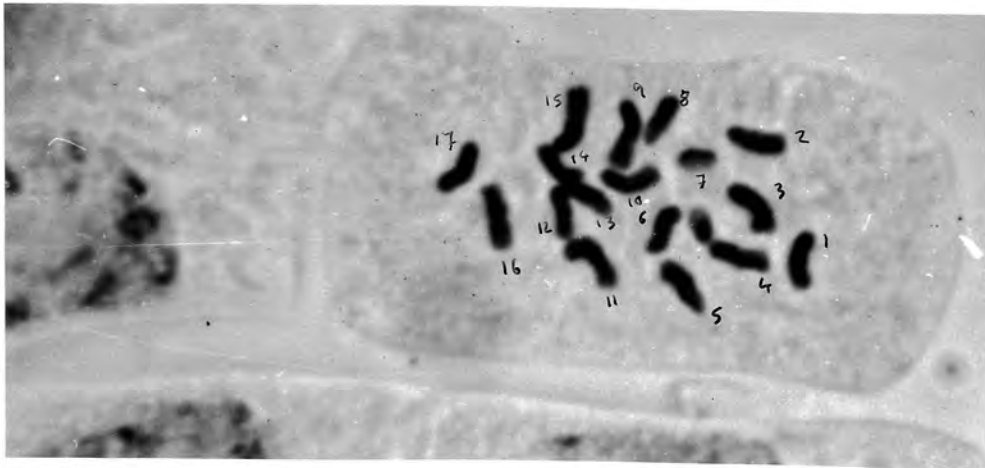


Type 'A'  1.8 u median
          2, 3, 5, 9, 10, 11, 15, 16, 17 = 9

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?
2,1.6   , median          = ?
3,2.2   , sub-median      = C?
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 Fixitive 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, Malecka (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 sum-
marised in Chapter 3. Perhaps the most outstanding feature of the combined
work were the repeated findings that all agamospermic species were poly-
ploid (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 facul-
tative 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 Gudjónsson 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 reproduct-

ion.  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 agamo-

spermy 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.

Furnkranz 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 Furnkranz claims.  In fact, the examination

of the pollen of plants of known chromosome number showed that whereas

Furnkranz'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    o
POLYPLOID  •
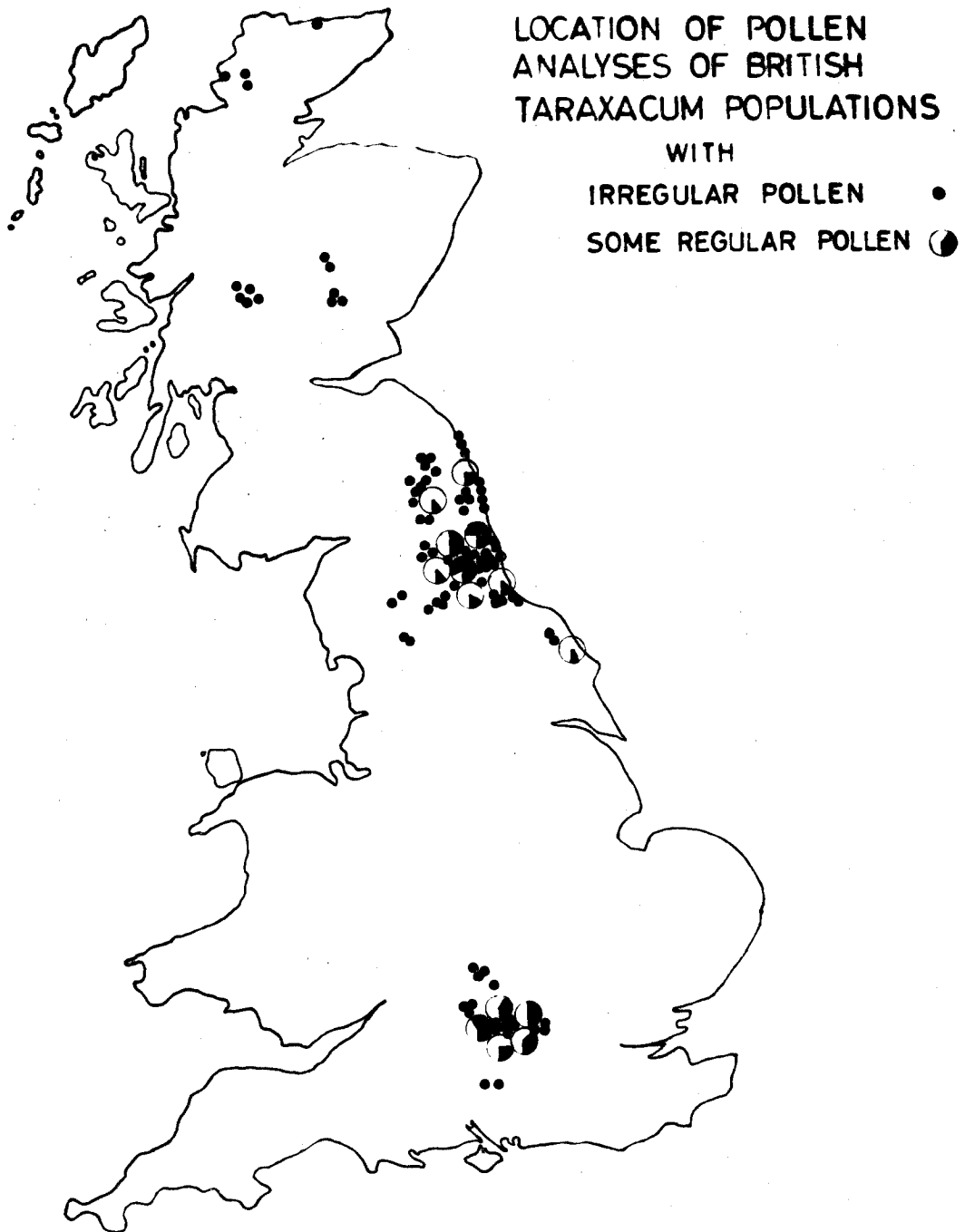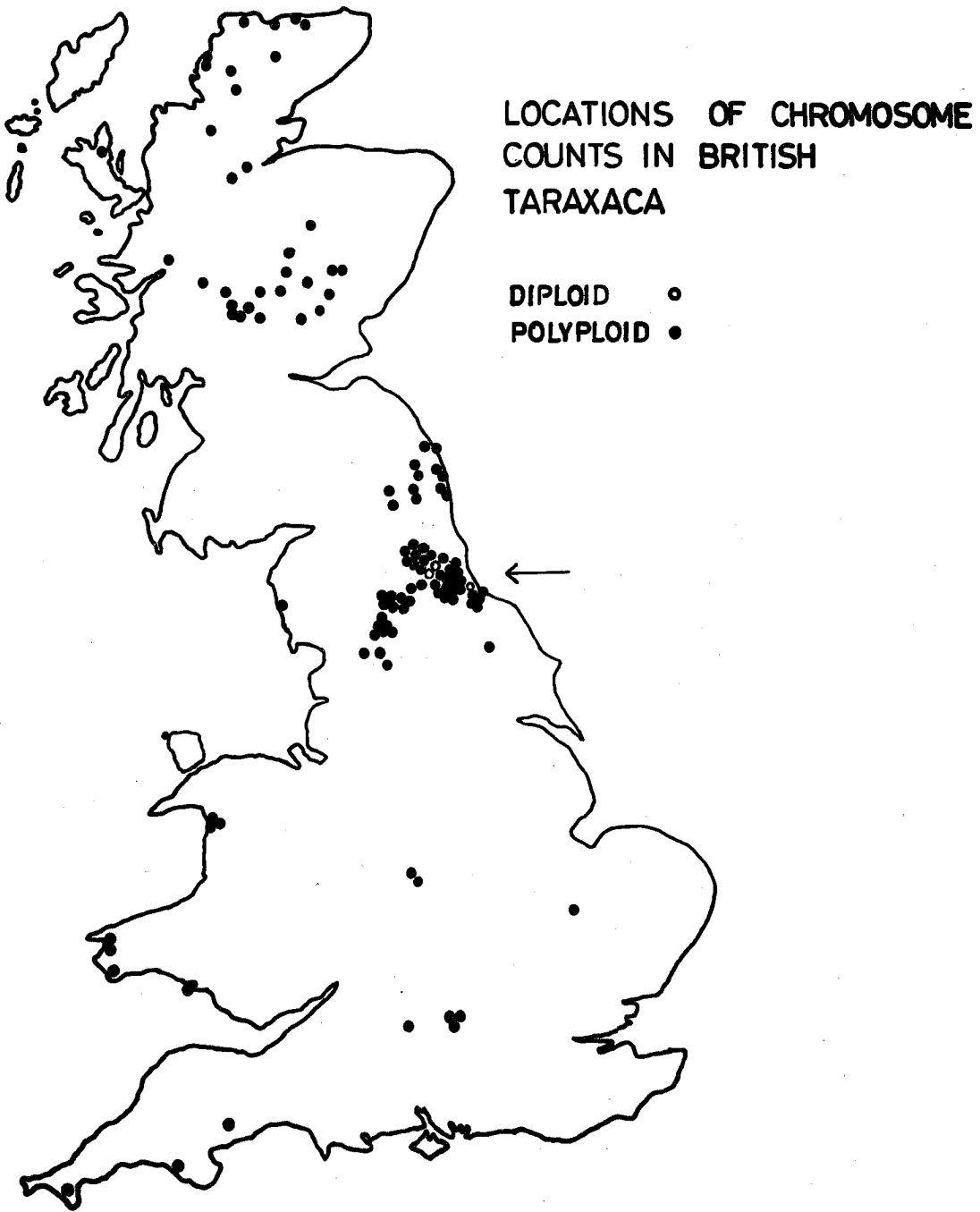
cytological examination is tabulated in detail in appendix 3, but they
are summarised below in table 14.

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.brachy-
glossum (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 Guðjónsson 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*<br>Sexual | | | | | | | | 1*<br>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 distribut-

ion 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

individuals of <u>T.isophyllum</u> 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 <u>T.isophyllum</u> 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 <u>T.isophyllum</u> from Kovacover Kopce appear as photographs 23 and 24. Professor van Soest, the <u>Taraxacum</u> 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.

148 DURHAM UNIVERSITY HERBARIUM
Name TARAXACUM
Habitat Sectie ERYTHROSPERMA D.Hl.
Calcareous grassland.
Locality Seven Sisters Eastbourne, C.S.62
Cult. Durham. 0.11.V
Collector 2n·16 3G
Det. Seen to self sterile Date 31.C.G.5

440 DURHAM UNIVERSITY HERBARIUM
Name Taraxacum
Habitat Sectie ERYTHROSPERMA D.Hl.
Calcareous grassland
Locality Seven Sisters taraxacum, C.S.62
Collector Cult. Durham.
2n·16 22. Altitude
Det. Mostly apomictic Date 1965

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

x 1/4

Photograph 24. As for photo-
graph 23, except that the plant
was triploid and apomictic.

x 1/4
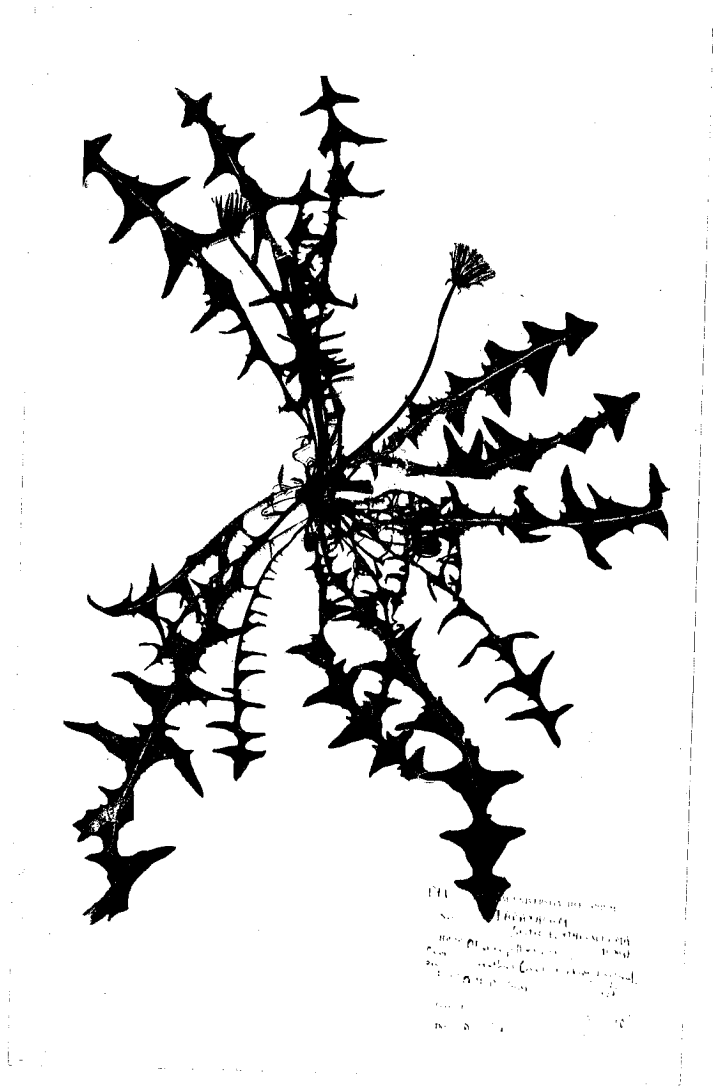
Photograph 25. Herbarium specimen of cultivated T.brachyglossum;
a facultative triploid with reductional pollen. Greatham Creek,
Co. Durham.

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 cleisto-gamous 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.brachy-glossum 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 restitution-al 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 | | |

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 |
|---|---|---|
| | 35 | 80 |
| | 35 | 80 |
| | 40 | 100 |
| | 45 | 100 |
| 164D | 55 | 100 |
| | 60 | |
| | 60 | |
| | 65 | |
| | 85 | |
| | 65 | 70 |
| | 65 | 70 |
| 171C | 85 | |
| | 95 | |
| | 100 | |
| | 70 | 85 |
| | 80 | 90 |
| 163A | 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 indistinguish-
able 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 ($\pm$ = 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 tetradtype 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 |
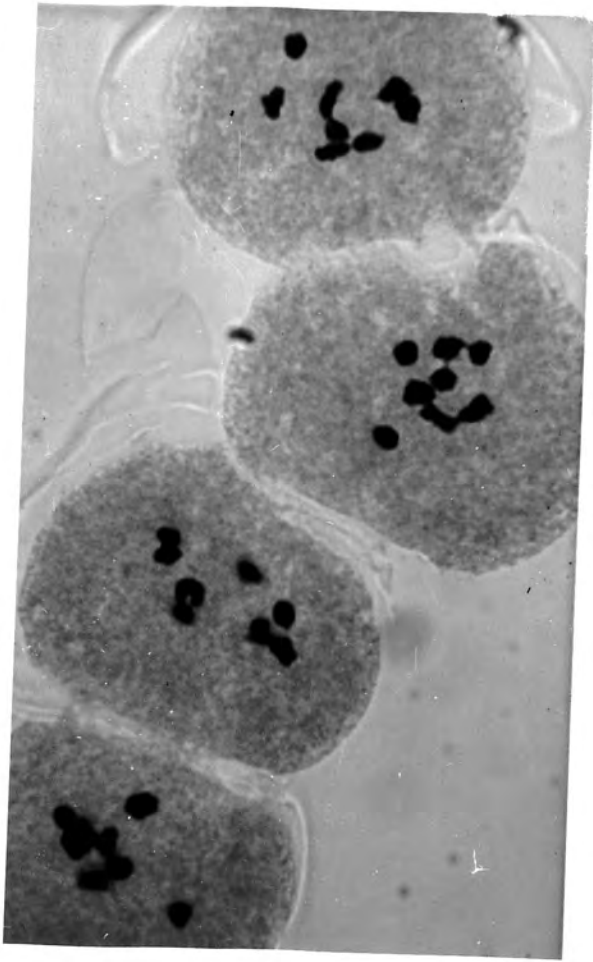
Photographs 26 and 27

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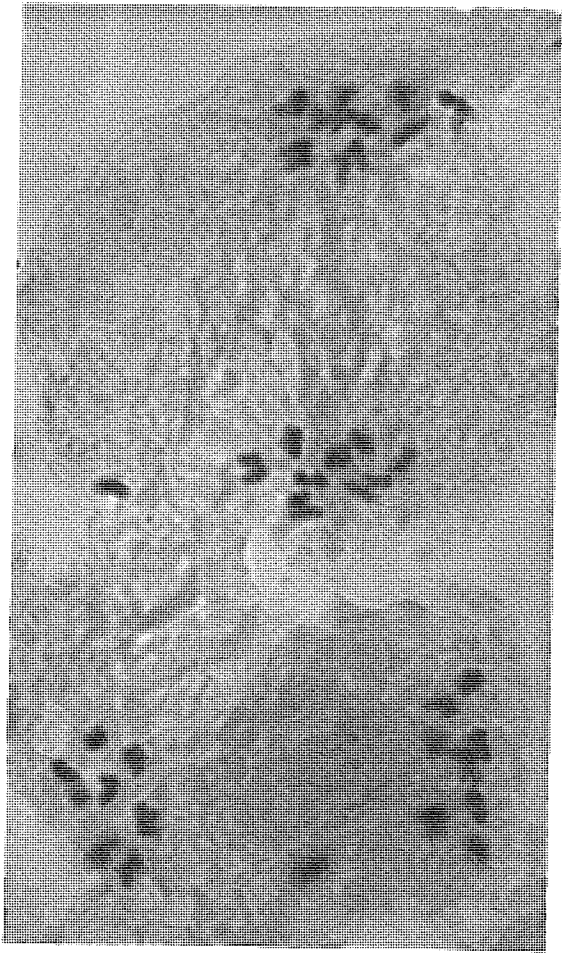
Photograph 28. Pollen mother
cell squash with Feulgen staining,
showing metaphase II in diploid
sexual T.bessarabicum, n=8

x 2000
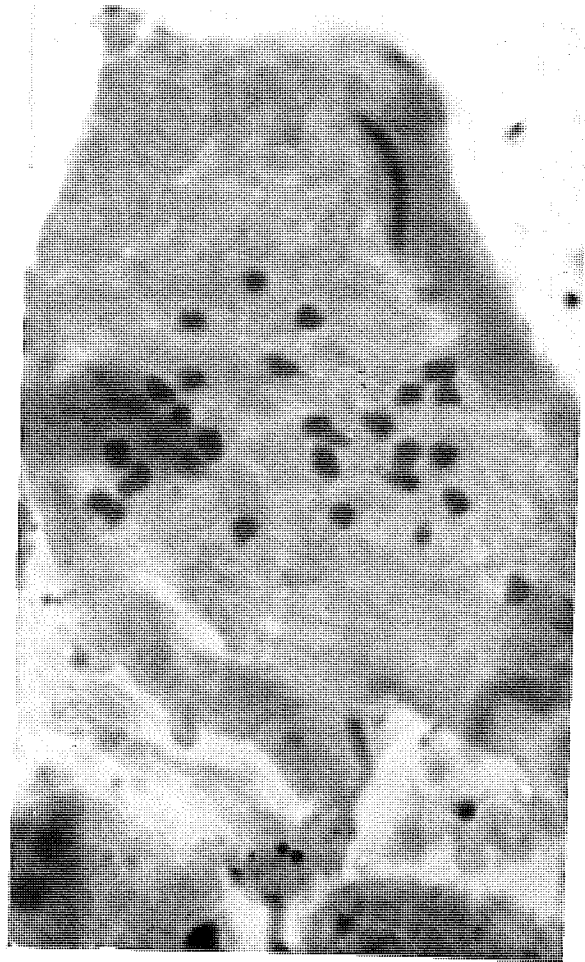
Photograph 29. Pollen mother cell
squash with mordanted aceto-
carmine staining showing metaphase
I in an asynaptic meiosis, n=24,
T.naevosum.

x 3000
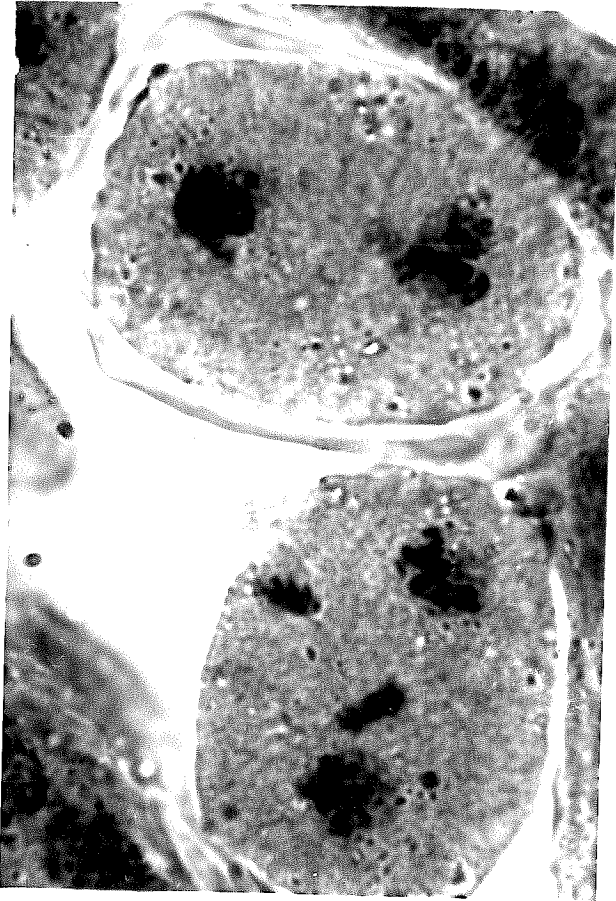
Photograph 30. Pollen mother cell
squash preparation with mordanted
acetocarmine staining showing
wholly and partially restitutional
telophase II in T.naevosum.

x 1200
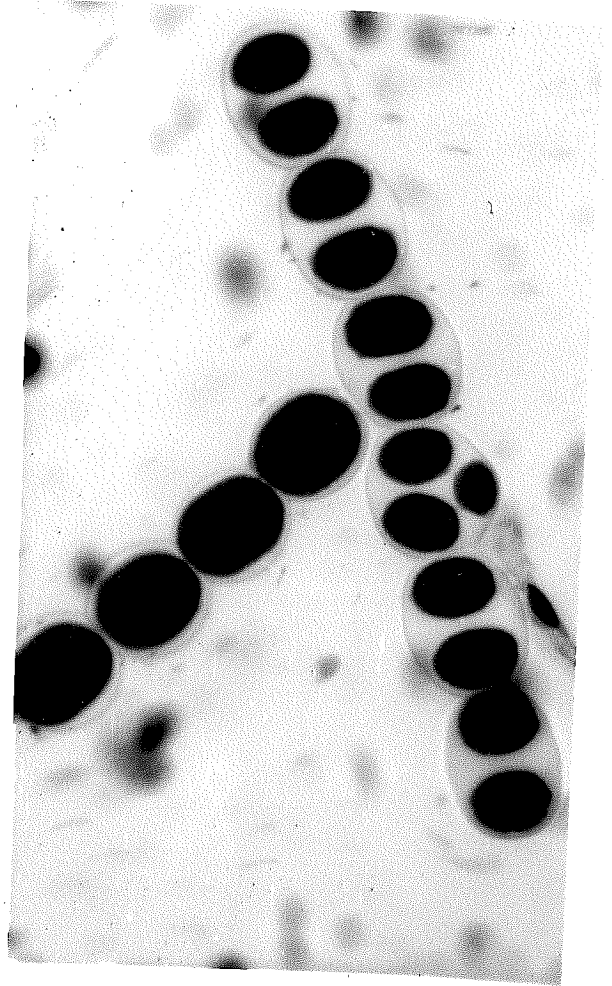


Photograph 31. Pollen mother cell
squash preparation with mordanted
acetocarmine staining showing
diads and triads in T.naevosum.

x 600
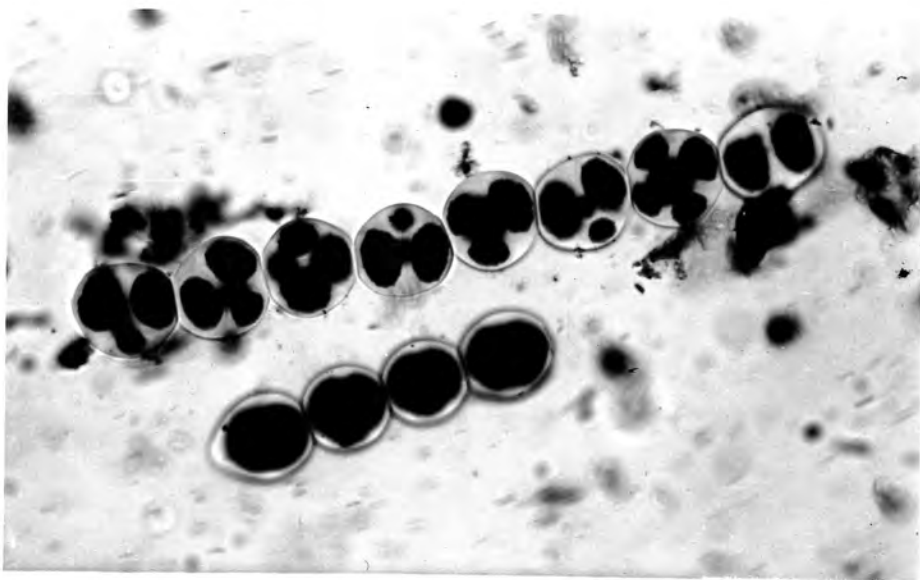
Photograph 32. Pollen mother cell squash preparation, with
mordanted acetocarmine staining showing irregular reductional
tetrad formation in triploid, facultatively apomictic T.
subcyanolepis.

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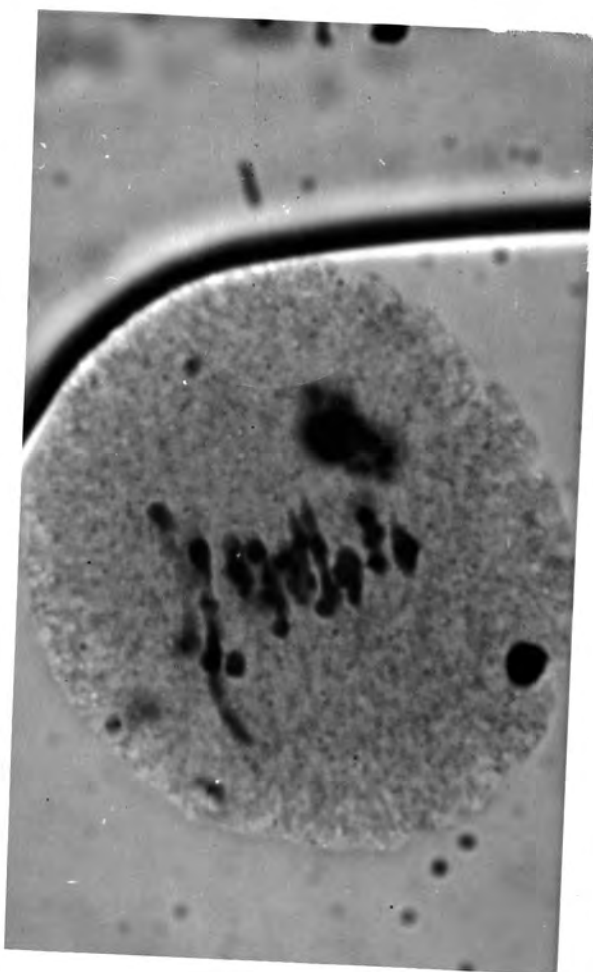
Photographs 33 and 34. Pollen mother cell squash preparation with Feulgen staining of meiosis in a colchicine-induced tetraploid T.isophyllum, n=16. Note regular pairing. This plant remained sexual, despite its polyploid condition.

x 3000
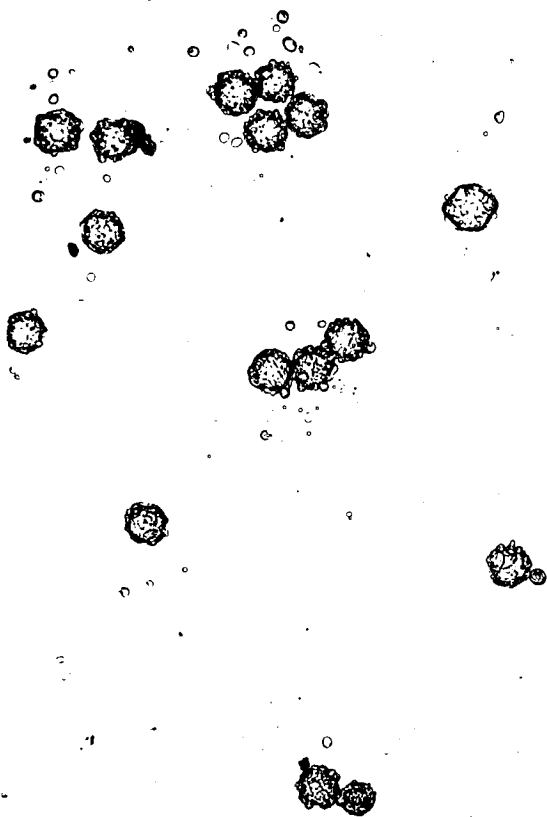
Photograph 35. Regular reductional pollen of triploid backcross from colchicine-induced tetraploid T.isophyllum.

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 inca-
pable 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 off-
spring resulting, the triploid pollen apparently contributes a genetic
system which allows the triploid unreduced egg-cell to develop preco-
ciously.

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 they possessed 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 restitut-

ional 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

\*     Diploid sexual ⟵——————————————→ hybridisation ⟵——————————→ \*Diploid hybrid, sexual

              autopolyploidy                               autopolyploidy

\*     Tetraploid sexual                                        (Tetraploid hybrid sexual or
                                                                sterile.)

              backcross to diploid

\*     Triploid sexual, or sterile

                      GENE SYSTEM A.  Precocious                 GENE SYSTEM A.  Precocious
                      embryogeny for unreduced                   embryogeny for unreduced
                      embryo-sacs.                               embryo-sacs.

\*     Triploid, facultatively  apomictic                                  (Tetraploid hybrid, facultative
                                                                   apomict.)

\*     Diploids arise regularly, and may become                         GENE SYSTEM B.
        established in a polymorphic relationship.                     Meiotic asynapsis

                                                  Tetraploid hybrid.
                                        \*     Obligate apomict.

                                         backcross of
                                         reductional pollen to
                                         diploid
                                                   \* Triploid hybrid
                                                   obligate apomict.

      evolution of obligate apomicts                      pentaploids, which are asynaptic
                                              and hexaploids, which may be very
      evolution of facultative                               irregular synaptic, probably arose
          apomicts.                                          from these points through chromo-
                                               some doubling and chance back-crossing

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

THE  KNOWN  DISTRIBUTION  OF  DIPLOID  SEXUAL  TARAXACA
IN  WESTERN EURASIA.

"Ancient" type wholly diploid species.

Wholly diploid species in mostly apomictic sections.

Populations showing diploid sexual/polyploid apomict
polymorphism.
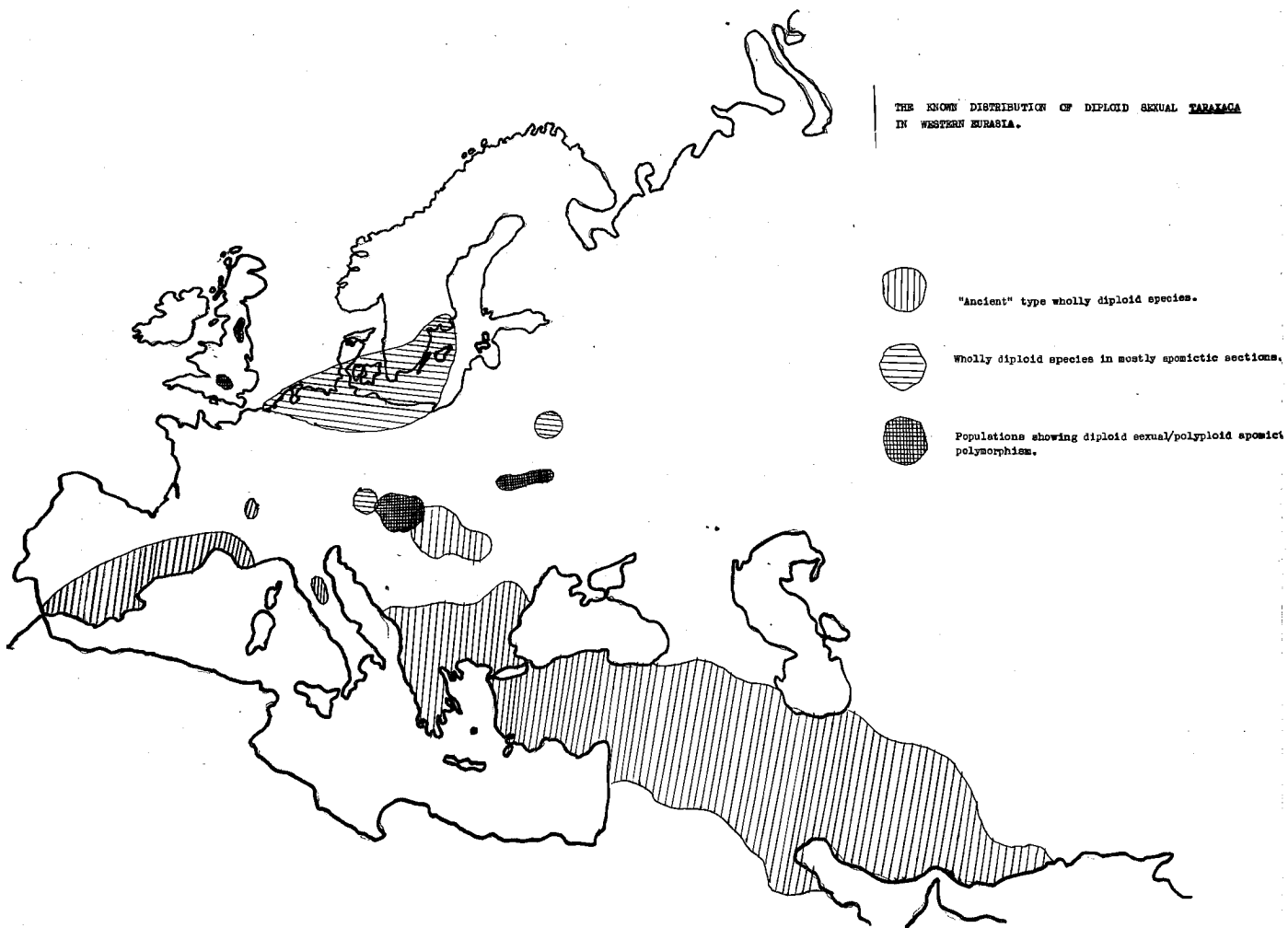
HYBRIDISATION

Very little hybridisation has been observed in <u>Taraxacum</u>, 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 <u>T.kok-saghyz</u>, <u>T.multiscaposum</u>, <u>T. bessarabicum</u> and <u>T.serotinum</u>, and she also crossed the pollen of the apomictic species <u>T.hybernum</u>, <u>T.brevicorniculatum</u> and <u>T.'officinale'</u> onto all of these sexuals. She found that <u>T.kok-saghyz</u> and <u>T.multiscaposum</u> 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. <u>T.officinale</u> might have been anything, including a tetraploid. Results from this work which are rather more curious are those regarding the other two sexual species, <u>T.serotinum</u> and <u>T.bessarabicum</u>. 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 hybridis-

ation 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 interme-
diate characteristics.    In his latest paper (1966) he uses his results to
destroy the biological foundation on which the justification of a micro-
species 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 resem-
ble 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 Gudjónsson (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 inter-

mediate 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 <u>T.serotinum</u>, <u>T.haussknechtii</u> and <u>T.bessarabicum</u> 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
<u>Diptera</u>, <u>Apis</u> and <u>Bombus</u> 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 |
| | T.brachyglossum 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.isophyllum | 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.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.polyodon | 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.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.duplidentifrons | T.brachyglossum 2n=24 | 1 | 50 |
| | T.isophyllum 2n=16 | 8 | 37 |
| | T.polyodon 2n=24 | 3 | 3 |
| | 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.brachyglossum 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.

## 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<br>Leaf dissected e. | E 9<br>e 5 | -? E |
| T.stevenii | Ligules striped red. L<br>Ligules striped grey I | L 3<br>I2 | -? L |
| T.isophyllum | Ligules striped dark puce      p<br>Ligules striped grey P | p 4<br>P 13 | P |
|  | Achenes purple      A<br>Achenes greyish      a<br>(f.achrycarpum) | A 9<br>a 4 | -? A (confirmed below) |
| T.austriacum | Ligules striped dark puce      p<br>Ligules striped grey P | p 4<br>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

$\frac{1}{4}$ 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 | ? Polygenic |
|---|---|---|---|---|
| 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 <u>Taraxaca</u> hybridising in the field are given by Furnkranz, 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 <u>Taraxacum</u> 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:

<u>Table 32. Hybrids recorded from herbarium material</u>

| 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 Furnkranz, 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.subcyanole-pis 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 inter-sectional identity:

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

   diameter of the capitulum, when the florets stand, or are held horizont-ally;

   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 jucture 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 populat-ions 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.

<u>Diagrams 11 and 12</u>

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 II

Seaton Carew  Durham

POPULATION  APOMICTIC

EXTERIOR  BRACT  LENGTH  →7·9MM. X

8·0MM.→ o

SCAPE  DIAMETER  MM

CAPITULUM  DIAMETER

Diagram 12.
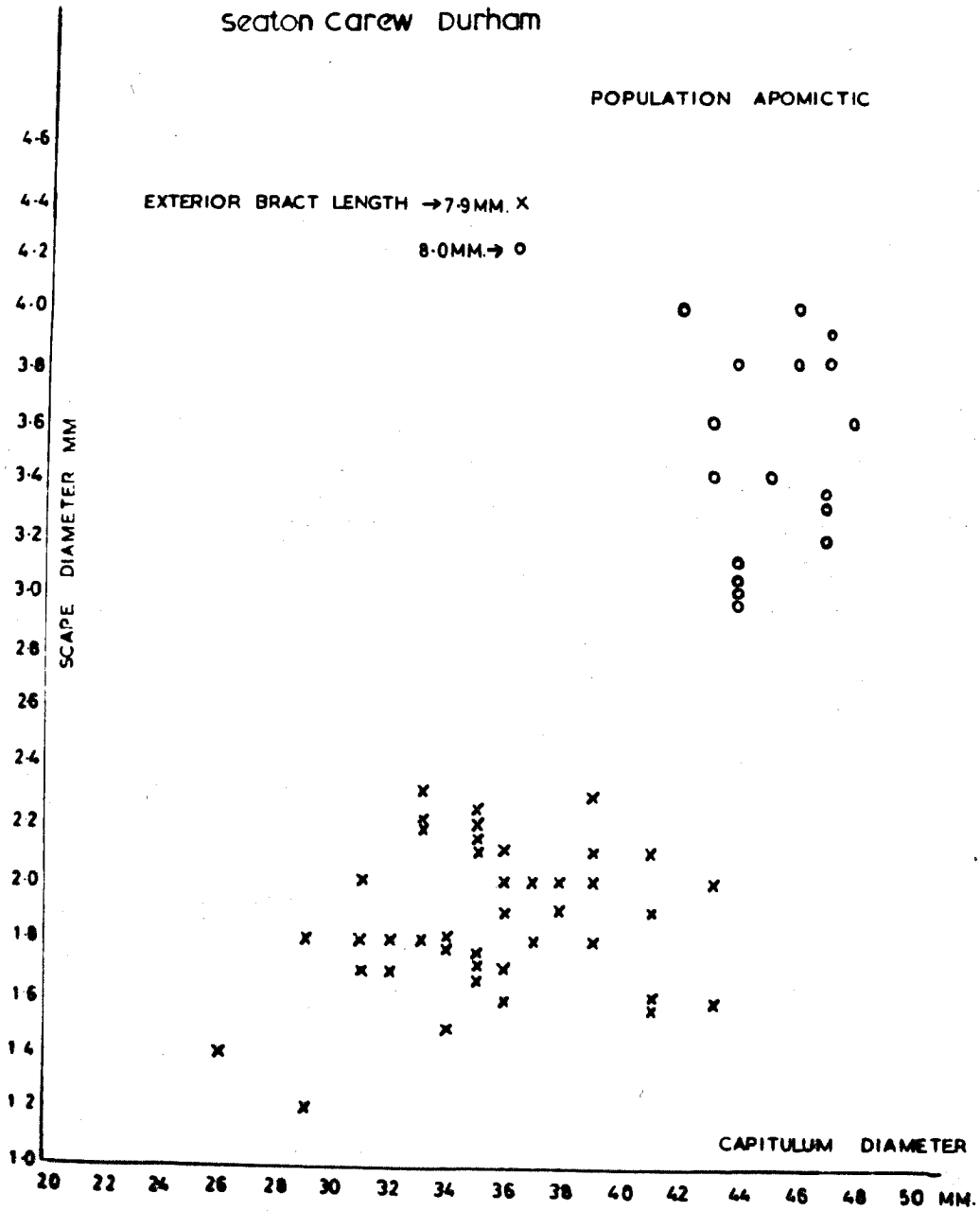
# Sherburn Hill Durham

POPULATION CONTAINING
SEXUAL PLANTS

EXTERIOR BRACT LENGTH → 7·9MM. X
8·0MM → O

CAPITULUM DIAMETER

SCAPE DIAMETER MM

MM
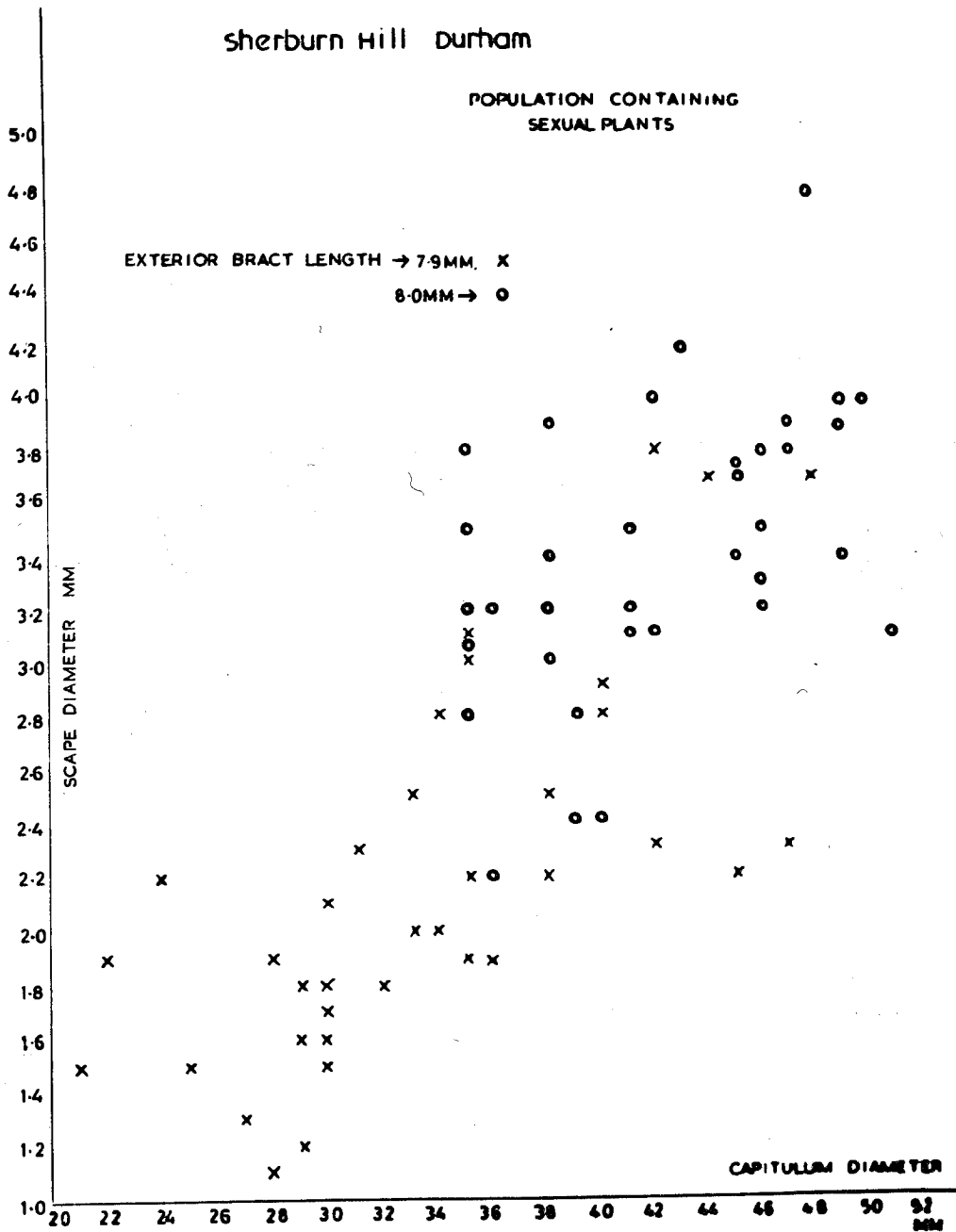
Table 33 (con.)

<u>Alnmouth, Northumberland.</u>  Grey dune system, dominated by <u>Agrostis stolo-</u>
<u>nifera</u>, but species-rich.

Species present:  <u>T.hamatum</u> (<u>Vulgaria</u>)

<u>T.brachyglossum</u> (<u>Erythrosperma</u>)

<u>T.brachyglossum</u> from this station has reductional pollen.  Regular
or near regular pollen is found in about 10% of this species. <u>T.hamatum</u> 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 pollinat-
ion of facultative and sexual <u>T.brachyglossum</u> with partially and totally
reductional pollen from <u>T.hamatum</u>.

---

<u>Bamburgh,Northumberland</u>. A grey dune system, similar to Alnmouth.

Species present: <u>T.hamatum</u> (<u>Vulgaria</u>)

<u>T.brachyglossum</u> (<u>Erythrosperma</u>).

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

Extensive hybridisation, with at least 40% individuals with hybrid
characteristics.  <u>T.oxoniense</u> 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 33 (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 charac-

ters 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 inter-mediates 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.

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.

NUMBERS OF SECTIONS
PER COUNTRY

KEY
5
10
15
more than 50%
totally
sexual
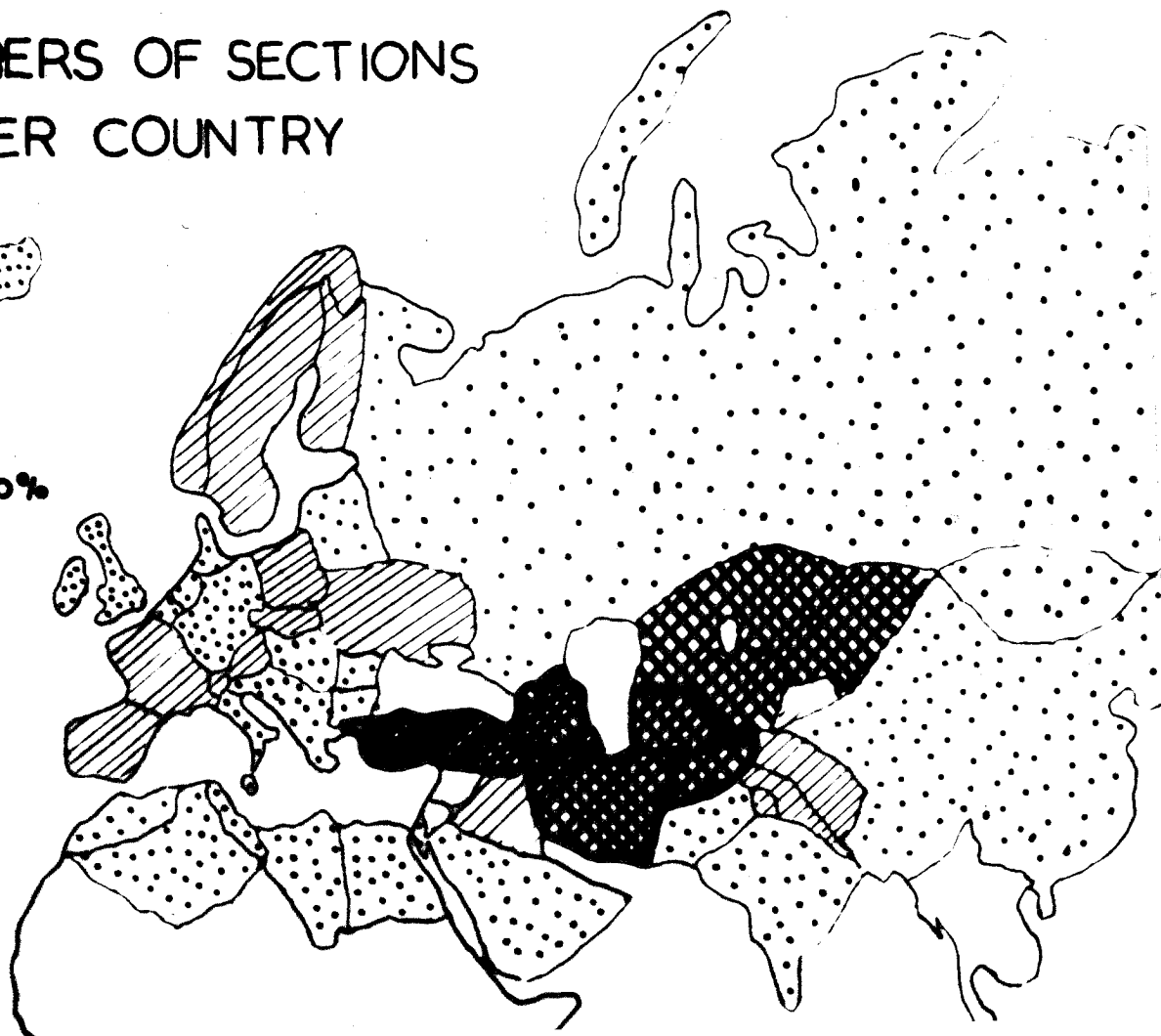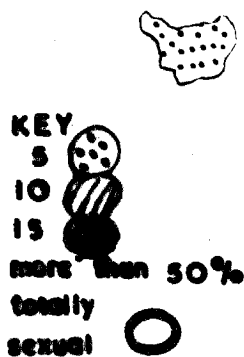
the Mediterranean. These sections have a number of rather less primitive characters, and furthermore they are self-fertile. They seem to represent an early evolutionary advance in the genus. The Glacialia may be a relict of a still earlier advance into the Mediterranean, when the primitive types were 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 dis-continuity 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
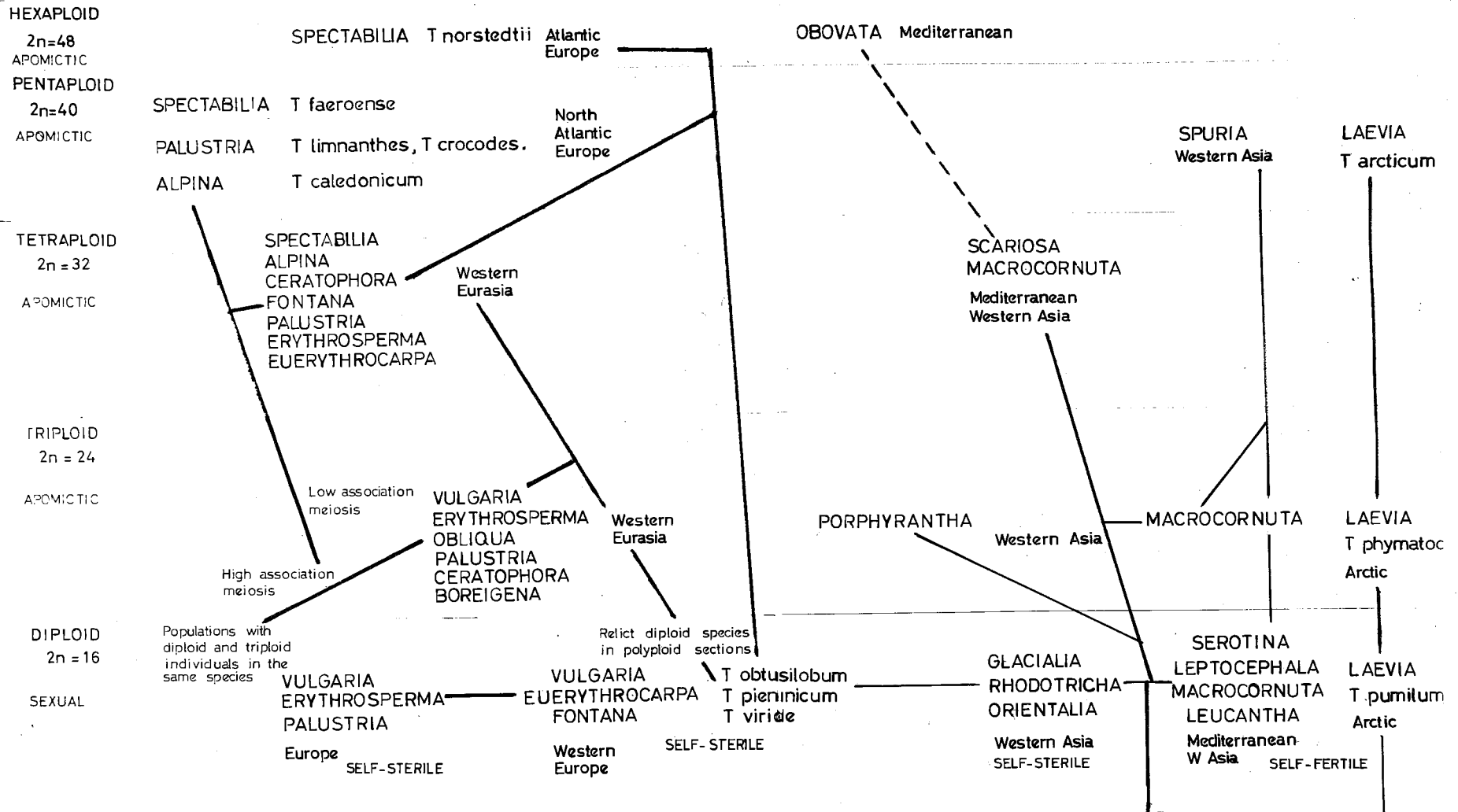
Table 32. The Primitive Sections of Taraxacum

| 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, 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 | |

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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 accom-

panied 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 environ-

mental conditions to be extant at the moment. No doubt the great plasti-

city 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 east-wards, 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 Erythro-carpa s.1., 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~~ this agrees with

Willis's age and area hypothesis.

INDEX OF NUMBER OF COUNTRIES.

SPECTABILIA AND ERYTHROCARPA
110 SPECIES.

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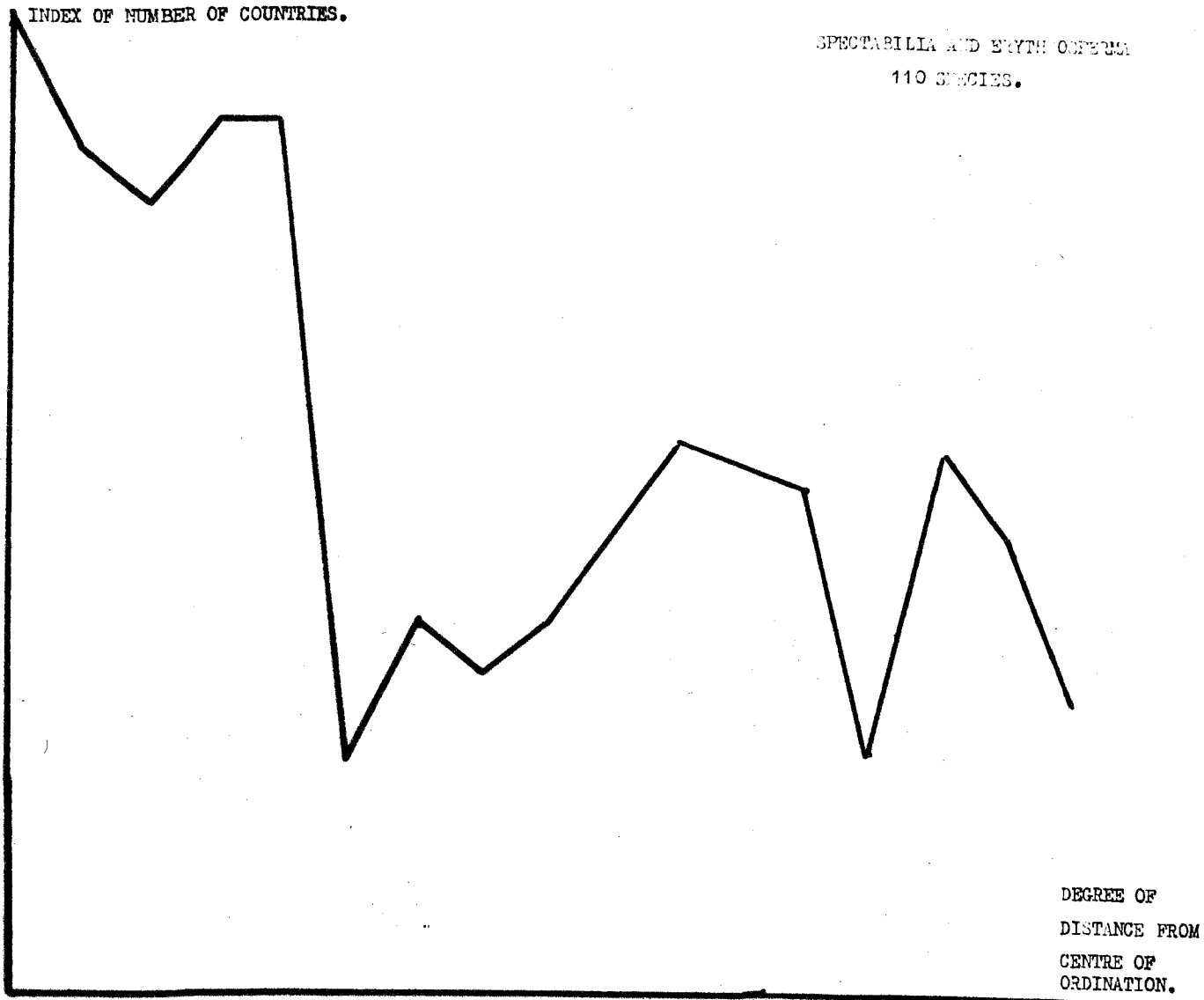
Graph 5. The number of countries in which species of the Spectabilia,
Palustria and Erythrocarpa s.1 occur, plotted against the distance
from the centre of ordinations at which they occur.

# 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 $20^{\circ}$C and at $1^{\circ}$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
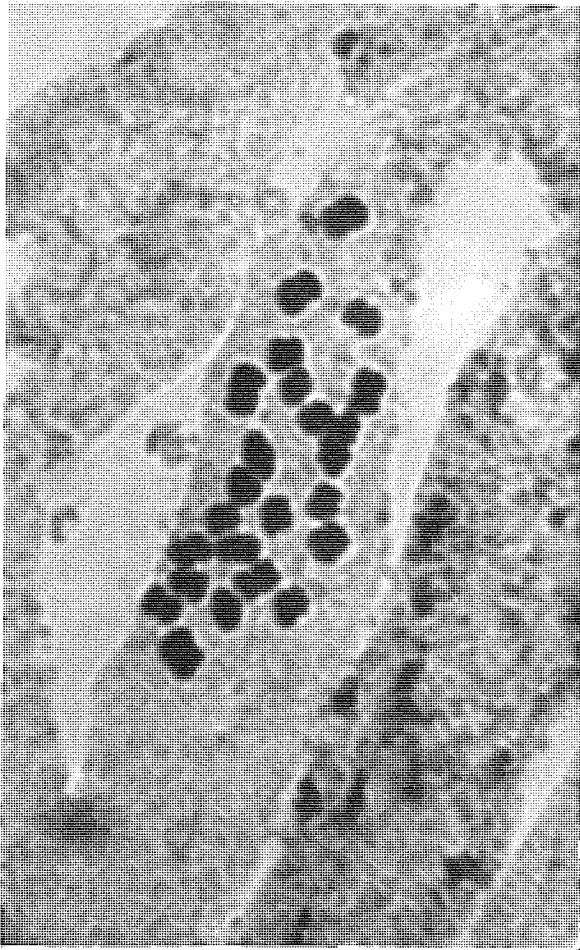
Photographs 37 and 38.  The effect of pretreatment with paradichlorbenzene
on root-tip squash preparation; T.undulatum, 2n=24; T.faeroense. 2n=40.

    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 $60^{\circ}$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 $60^{\circ}$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 soften-ining 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 embryo-logical 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 tech-

nique 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 $30^\circ$C for 2 days in chloroform, and increasing

amount of paraffin wax.

5.   Incubate heads for 5 hours at $60^\circ$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 $60^\circ$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 cotyledors 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

<u>Genera:</u> 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.

<u>Species:</u> Agrostis stolonifera L.

Festuca ovina L.

Poterium sanguisorba L.

<u>Taraxacum Weber</u>

| <u>Section:</u> | <u>Species:</u> |
|---|---|
| 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.bessaribicum (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

minimum

| | | | |
|---|---|---|---|
| T.~~bithynicum~~ | (621) | 2n=16 + 0 | 25MN.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

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

Section Fontana

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

Section Palustria

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

Section Spectabilia

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

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, Northumber-land, 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 + O         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 + O           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 + O           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 + O                Roadside, Bonar Bridge, W. Ross;
                                            3-6-1965, A.J.R.

    T.dentilobum  (593) 2n=24 + O, 3S       Garden, Les Saintes-Maries de la
                                            Mer, La Camargue, Provence, France,
                                            8-1966, A.J.R.

    T.duplidentifrons (135) 2n=16,24        Limestone grassland, Hlohovec, C.S.S.R.
                           (siblings)       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.monochlamydemeum  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 + O | 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 + O | 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 + O-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,+O-3S | Richards |
| T.proximiforme | 2n=24 | Richards |
| T.pseudolacistophyllum | 2n=32 | " |
| T.argutum | 2n=24 + OS | " |
| T.silesiacum | 2n=23,24, +1,2,3S | " |
| T.simile | 2n=32 + OS | " |
| T.friesii | 2n=32 + OS | 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.nordstedtii | 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 <u>Vulgaria</u> (con.)

| | | |
|---|---|---|
| T.<u>involucratum</u> | 2n=24 | Gustafsson 1933 |
| T.<u>latissimum</u> | 2n=24 | " |
| T.<u>croceiflorum</u> | 2n=c.20 | " |
| T.<u>laciniosifrons</u> | 2n=19,20,22,23,24,48 | Sörensen and Gudjónsson 1946 |
| T.<u>polyodon</u> | 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.<u>cordatum</u> | 2n=23,24 | Sörensen and Gudjónsson 1946 |
| | 2n=24 | Richards |
| T.<u>hamatum</u> | 2n=24 | Sörensen and Gudjónsson 1946 |
| T.<u>subcyanolepis</u> | 2n=16,18,20,24,25,26,27,28,29 | Richards |
| T.<u>speciosum</u> | 2n=24 | Richards |
| T.<u>bracteatum</u> | 2n=23,24,25 + 0-1S | " |
| T.<u>hamiferum</u> | 2n=24 + 2B | Richards |
| T.<u>alatum</u> | 2n=24 +0, 2, 3S | " |
| T.<u>cyanolepis</u> | 2n=24 + 0 | " |
| T.<u>dentilobum</u> | 2n=24 + 0, 3S | " |
| T.<u>pseudohamatum</u> | 2n=24 + 0S | " |
| T.<u>microcarpum</u> | 2n=24 + 0S | " |
| T.<u>oreinicolum</u> | 2n=24 + 2-3S | " |
| T.<u>acutangulum</u> | 2n=24 + 2S | " |
| T.<u>duplidentifrons</u> | 2n=24, 16 | " |
| T.<u>sellandii</u> | 2n=28 | " |
| T.<u>klingstedtii</u> | 2n=22,24,25 + 1-3S | " |
| T.<u>dahlstedtii</u> | 2n=27,24 | " |

Species Incertae Sedis

| | | |
|---|---|---|
| T.<u>nutans</u> | 2n=16 | Poddubnaja-Arnoldi and Dianova 1934 |
| T.<u>robustum</u> | 2n=24 | " |
| T.<u>samuelssonii</u> | 2n=32 | Gustafsson 1935B |
| T.<u>confertum</u> | 2n=16 | " 1933 |
| T.<u>nigricans</u> | 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 + O | Richards |
| T.isophyllum x T.fontanum | 2n=17,18,19 + O | " |
| T.polyodon x T.litorale | 2n=21,23 + OS, 2S | " |
| T.isophyllum x T.succulenteum | 2n=16,18,19 + O-2S | " |
| T.viride x T.succulenteum | 2n=18, + 1S, 20+O | " |
| T.viride x T.polyodon | 2n=17, 18 + O -1S | " |
| T.isophyllum x T.cimbricum | 2n=16,18,21 + O-1S | " |
| T.viride x T.brachyglossum | 2n=17, 18,20 + O-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

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# 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:

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

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

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