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SPONTANEOUS CHROMOSOME-ABERRANTS IN APOMICTIC TARAXACA

MORPHOLOGICAL AND CYTO-GENETICAL INVESTIGATIONS

BY

THORVALD SØRENSEN AND GUÐNI GUÐJÓNSSON

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Fig. 1. Cultures of *Taraxacum laciniosifrons* Wiinst. aberrants in the experimental fields of the Botanical Garden of the University, Nørre Fælled. Photogr. May 16, 1940.

I. CULTIVATION EXPERIMENTS AND MORPHOLOGY

BY

THORVALD SØRENSEN

I. Introduction.

The interest taken in the study of apomictic species has constantly increased during the last few decades. The taxonomic value that should be given to the apomictic units has always been a matter of dispute. The question has been regarded as a purely conventionally systematic one, for unlike what is the case with the sexual species, we can have no hope of approaching the problem by way of genetics. Thus a sufficient experimental basis for a final estimate of the taxonomic value of the apomictic microspecies can scárcely be procured. However, already Ostenfeld's pioneer investigations of the species formation in *Hieracium* (1910, 1912) in conjunction with Rosenberg's collateral cytological investigations (1917) should warn us to be cautious in drawing general conclusions concerning the nature of the apomictic species and the genetic and systematic value of the individual biotypes.

The idea of the constancy of the apomictic microspecies and the assumption of their distinct occurrence in nature, have gradually assumed the character of a dogma to apomict systematists. However, no outsider is immediately capable of estimating, to say nothing of criticising, what is seen by the trained eye of the specialist. MARKLUND (1938, 1940) maintains very vigorously that the mutual differences between the apomictic species, at any rate within the genus *Taraxacum*, are of a different and more radical character than between biotypes of sexual species. And yet, taraxacologists are by no means agreed as to the delimitation of the concept of species. Owing to the excessive modificative variability characterising *Taraxacum*, it will be quite impossible immediately, during the investigations in the field, to demonstrate the smallest genotypically determined differences. As regards the forms of the *Alchemilla vulgaris* group, the modificative variability of which is more limited, the monotypy of the microspecies has previously been distrusted, and recently it has been shown experimentally by TURESSON (1943) that a number of Scandinavian *Alchemilla* microspecies comprise several genetically distinct types.

The experience gained so far of the hereditary conditions of the apomicts must, however, be said to support the assumption of a relatively high degree of constancy in these species, as compared with the amphimicts. From cytological quarters (DARLINGTON 1932, 1937, GUSTAFSSON 1934) it has, however, been pointed out that in forms in which there is no question of nucellar embryony but of actual parthenogenesis, as for instance in *Taraxacum*, there is a theoretical possibility of the segregation of new combinations of genes similarly as in the amphimicts, if traces of meiotic phenomena are still left in the formation of the embryo sac and the egg cell. GUSTAFSSON (1934) is of opinion, on the basis of his comprehensive cytological investigations of *Taraxacum*, that the observations made by him strongly favour the assumption of the development of new forms by a so-called pseudomutation. By this he means 1) non-disjunction during the "pseudohomotypic" meta- and anaphases preceding the formation of the non-reduced embryo sac, which will give rise to mutants differing in a number of characters (new species), and 2) crossing-over in the prophase, which will only result in insignificant deviations in the genotype. However, GUSTAFSSON has observed no differentiation of new types in his experimental material.

MARKLUND (1940) has made a careful study of the *Taraxacum* flora of southern Finland. The complete absence of endemic species within the natural plant communities is interpreted by MARKLUND as a proof of the probability that not a single species has originated here since the Ice Age. Even though this conclusion may not be valid, MARKLUND's floristic investigations are at any rate suggestive of the comparative antiquity of the species in question, and of a high hereditary constancy. Species with a very sparse distribution in Finland but otherwise unknown, are, however, not absent, but such species are chiefly associated with cultivated fields. MARKLUND regards these species as recently introduced from regions the *Taraxacum* flora of which has not yet been closely investigated.

Quite recently M. P. CHRISTIANSEN (1942) has described the *Taraxacum* flora of Iceland. By far the majority of the 116 species in Iceland are endemic, and a large number of species seem even to have a fairly limited area of distribution in Iceland. Although future investigations of the *Taraxacum* flora of the North Atlantic regions will possibly reduce the number of endemisms to some extent, the only possible consequence of CHRISTIANSEN's results seems to be that a fairly lively differentiation of forms must have been going on in Iceland after the Ice Age, or perhaps only since the Norse colonisation about a thousand years ago, the greater number of them being associated with túns (home-fields). Now I wonder whether the disagreement between the results of the two taraxacologists is not to be found, at any rate partially, in a different delimitation of species. And will all MARKLUND's presumed old species pass muster before the isoreaction test, which is regarded by CHRISTIANSEN (1942, p. 243) as an indispensable requirement. Whether the very narrowest conception of species, as advocated by CHRISTIANSEN, or a more ample conception should be preferred, the future may decide. For the experimental demonstration of alterations, if any, of the genotype, a valuation of the smallest differential characters is *a priori* an absolute necessity.

In 1936 the present author commenced an investigation on the Danish *Taraxaca* based on field studies and cultivation experiments, with the object of trying to elucidate the problem of the development of forms within this genus so rich in apomictic forms. Owing to the great abundance of forms within the genus *Taraxacum* and the remarkable difference in the biotypes at hand within relatively very small geographical distances this genus must *a priori* be regarded as especially suited for such studies.

Even the initial experiments with transplanting of a number of microspecies from various localities and the sowing of seeds of the experimental plants for observation of series of plants of the same age and stage of development were a great encouragement to continue the study. The supposition of the very rare occurrence of "monofactorial" varieties within the apomicts proved to rest on an insufficient basis. For in a number of cases it was possible to ascertain differences between the clones within the same microspecies. However, the differences were mainly quantitative and of such an order of magnitude that they are indeed readily observable in the plants cultivated in rows in the experimental field, but if one would attempt to give an exact description of the plants, one will be at a loss. In a few cases the points of difference were, in fact, of a more tangible nature. The taraxacologists will here, probably with good reason, speak of erroneous determinations and of new species. Thus the aforementioned experimental results alone will hardly serve as a basis for a justifiable criticism of the established delimitation of the microspecies.

More surprising, however, was the occasional occurrence of individuals which differed so greatly from the type that they could hardly be referred by specialists to the main form. In 1940 the present author published a preliminary note on these results. The experiments have been continued since then, comprising a greater number of species, and have confirmed the results first arrived at.

In the course of the last few years Mr. G. GUÐJÓNSSON has joined the investigation as a cytological collaborator. The cytological results arrived at so far have been of decisive importance, and together with the continued cultivation experiments they have given rise to a number of problems, but by far not all of these are dealt with in the present work. Thus in the present paper we shall principally deal with a single series of aberrant types whose nature is fairly easily perceptible cytologically, but which—it must be admitted—in the first instance, at any rate, hardly contribute to elucidate the problem of species formation.

2. Experimental Methods.

The experimental methods are of the simplest possible kind. As a rule the seed was sown immediately after ripening in the month of June in flower-pots which were placed in a hot-bed. Sterilised soil was not used. To safeguard against the admixture of false plants which might arise from seeds present in the soil, the pots filled with soil were placed in the hot-bed two or three weeks before the seeds were sown. Weeds sprouting before that time were removed. Since *Taraxacum* sprouts very rapidly under the given circumstances—the seedlings appearing in the course of a week—false *Taraxacum* seed in the soil, if any such were present, would have sprouted long before the sowing of the experimental seed. It has turned out, however, that the probability of the presence of germinable *Taraxacum* seed, which has survived during the winter in the soil employed, is practically nil. The seed sown in all the primary experimental series was derived from plants which had been transplanted into the experimental garden from their natural habitats one or several years before. When the seedlings had developed their first foliage leaf, they were pricked off into flat boxes, about a hundred in each. After developing a small leaf rosette, the plants were planted in the open in rows at intervals of c. 15 cm. This planting into the open may take place as early as the end of July. By this procedure it is possible to obtain one generation a year for observation, as the plants treated in this way will be able to produce large and normally developed leaf rosettes in the course of the late summer. They will then yield vigorous flowering plants next spring. Even the autumnal leaf rosettes are so typical and uniform that aberrants, if any, can be readily pointed out.

Sowing in the summer, as described here, presents several advantages over sowing in the spring, viz. 1) one generation a year for observation will be secured; 2) the germinating power of the seed is greatest immediately after ripening, after which it will rapidly diminish; 3) sowing in the summer will yield more harmoniously developed, typical and uniform plants than sowing in the spring, which will frequently result in too vigorous rosettes, which will possibly flower already in the autumn of the first year. However, there is the drawback about sowing and planting in the summer that the young plants, after being planted in the open, are often exposed to attacks by wire worms, against which it may be necessary to take measures. The effects of an attack on the young plants constitute a serious obstacle to the later demonstration of aberrants, since the gnawed off plants will as a rule regenerate. The leaves of the new proventive rosettes assume a more juvenile character, apart from the fact that the plants themselves are weaker than the intact ones and may accordingly easily be mistaken for weak deviating individuals.

As already stated in a preliminary note (1940), the presence of deviating plants in seed progenies of several species of common occurrence in nature is no rare thing, it is even rather the rule. The reason why this fact seems hitherto to have escaped the attention of taxonomists working experimentally may be that in addition, probably, to having too small a number of plants, they have made an unconscious selection within the plant material already during the pricking off. As a rule, though indeed not always, the aberrants are from the outset weaker than the normal plants. Provided that a larger number of plants than is required for planting have sprouted, any gardener will instinctively use the most vigorous specimens and throw away the weaker ones and accordingly the aberrants, if any.

The experiments were largely made with the microspecies *T. laciniosifrons* Wiinst. and *T. polyodon* Dahlst. In addition, a great many other species were cultivated in such large numbers that the possibilities of a formation of different forms in these, both qualitatively and quantitatively, could to some extent be estimated.

To facilitate the orientation in regard to the segregation phenomena a preliminary survey of the most important experimental results treated in the present paper will be given below:

1) On cultivating a sufficiently large number of individuals it turned out that a great many species produce a number of aberrant types. It is shown in the present investigation that the great majority of these types are aberrants in the strict sense of the word, i. e. plants deviating in chromosome number from the typical ones.

2) Each species segregates again and again identic, or very nearly identic, aberrants.

3) Various species to a great extent segregate analogous aberrants, producing well defined aberrant types. Accordingly the aberrant types constitute parallel series, which transgress the specific limits.

4) The aberrants of the first order (primary aberrants) produce aberrants of a higher order in the filial generations. These form parallel series to the primary aberrants.

5) The frequency of the formation of new types varies from species to species.

3. Description of the Aberrant Types.

The cytological examinations of the plant material have provided a rational basis for a grouping of the aberrant types. It should, however, be mentioned at once here that the division on a cytological basis coincides in broad features with a division which had presented itself beforehand as a result of a morphological and a genetical estimate of the aberrants.

All the species employed as original material belong to the *Vulgaria* group with the chromosome number $2n = 24$. Earlier cytological investigations (Gustafsson 1932) have shown that the basic number within the genus is $x = 8$. Thus it has been rendered probable that the *Vulgaria* forms are triploid (cf. further the cytological part, p. 33).

On the basis of the determinations of chromosome numbers the observed aberrant plants can be divided into the following groups:

A. Aneuploid chromosome aberrants.
   1) Aberrants with a reduced chromosome number (hypoploid aberrants).
   2) Aberrants with an increased chromosome number (hyperploid aberrants).
B. Aberrant plants with an unaltered chromosome number (possibly complex mutations and point mutations).
C. Polyploid aberrants.

As pointed out above, certain types of aberrants occur analogously in a number of microspecies. These aberrants, which must accordingly be said to occur with a certain regularity, are in addition by far the most frequent. They proved to belong to group A 1, hypoploid aberrants, and group C, polyploid aberrants. Only these types of aberrants will be described in more detail in the present paper.

A. Aneuploid Chromosome Aberrants.

1. Aberrants with a reduced chromosome number (hypoploid aberrants).

a. Primary aberrants ($2n = 23$).

Eight $2n = 23$ aberrants, well distinguished morphologically, have been observed. The cytological basis for these aberrants is clear in so far as it has been possible by comparison with the chromosome complement of the normal plant to identify the lacking chromosome with a high degree of probability for each single aberrant (cf. the cytological section, p. 35). According to the most conspicuous characters, mainly regarding the stature of the plant or the shape of the leaves, they are here denoted as follows: 1) *aberr. elegans*, 2) *aberr. truncata*, 3) *aberr. plumosa*, 4) *aberr. hamosa*, 5) *aberr. pygmaea*, 6) *aberr. tenuis*, 7) *aberr. olivacea*, 8) *aberr. crassifolia*. The first-mentioned five aberrants were observed in a fairly large number of species, while the last three have hitherto only been observed in very few or a single species.

Aberrants of this group are so characteristic that on the basis of the leaf rosettes alone they can be determined with the same certainty as that with which the good species can be identified. This applies irrespectively of whether they originate from one or the other species. However, to what species they belong can only be ascertained by observation of the floral characters, and even these will often leave one at a loss in cases in which uncontrolled aberrants have arisen. Thus it has so far been impossible to refer with certainty to their proper main species several aberrants found in nature and later cultivated, e. g. *aberr. truncata* and *aberr. plumosa*. Only the "production" under control of identic aberrants can finally settle the question.

Referring the reader to the illustrations, a description will be given below of each of the eight 2 n = 23 aberrants, stress being merely laid on the differential characters as compared with the corresponding main species.

1) *Aberr. elegans* (Pl. I, b and g; Pl. VI, c, C and m, M; Fig. 2, b; Fig. 3, b; Fig. 4, b, g). The colour of the foliage is a fresh light-green, almost as in *T. longisquameum* Lindb. f. The position of the rosette leaves is a little more erect, the leaf form shows straighter lines, the interlobes being longer, the terminal lobe as well as the lateral lobes have a more concave front edge (less markedly claw-shaped in aberrants of species with this property), and more narrowly pointed and almost without small secondary teeth. The stalks of the flower-heads are inconsiderably longer and more slender, the flower-heads are a little smaller, the outer leaves of the involucre somewhat more deeply purple-coloured and a little longer, often with a tendency to have several leaves adhering in groups. In some few cases the scape issues almost from its middle a side branch from the axil of a small bract, the scape being thus bifurcate; the side branch is then a little weaker, and its head a little smaller than that of the main scape. This character has never been observed under cultivation in any other aberrant or in any Danish species and should not be mistaken for the phenomenon frequently observed that vigorous plants carry a double head on a normal or fasciated scape. The young plants of the first year show a fairly great tendency to develop lateral rosettes. In the normal plant, and in the other aberrants also, lateral rosettes do not, as a rule, arise till the second year, simultaneously with the flowering. *Aberr. elegans* is the earliest-flowering of them all. The flowering always sets in 5—8 days earlier in the spring than in the normal plants of the same species. The cell size is normal. The achenes are a little smaller than in the normal plant, the pyramis[1]) short and broad, less sharply delimited from the achene itself. The colour of the achenes is somewhat yellowish or brownish, especially towards the apex. Seedlings slightly more slender than in the normal plant. Fertility noticeably reduced, the heads always containing a relatively large number of empty achenes.

Aberr. elegans has been observed under cultivation in the following species: *T. laciniosifrons* Wiinst., *T. polyodon* Dt., *T. expallidiforme* Dt., *T. pannulatum* Dt., *T. chloroleucum* Dt., *T. privum* Dt., *T. sublaeticolor* Dt., and *T. intumescens* Hagl. *Aberr. elegans* has been found twice in nature (and cultivated), one evidently belongs to *T. vitel-*

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[1] Terminology according to Dahlstedt 1921.

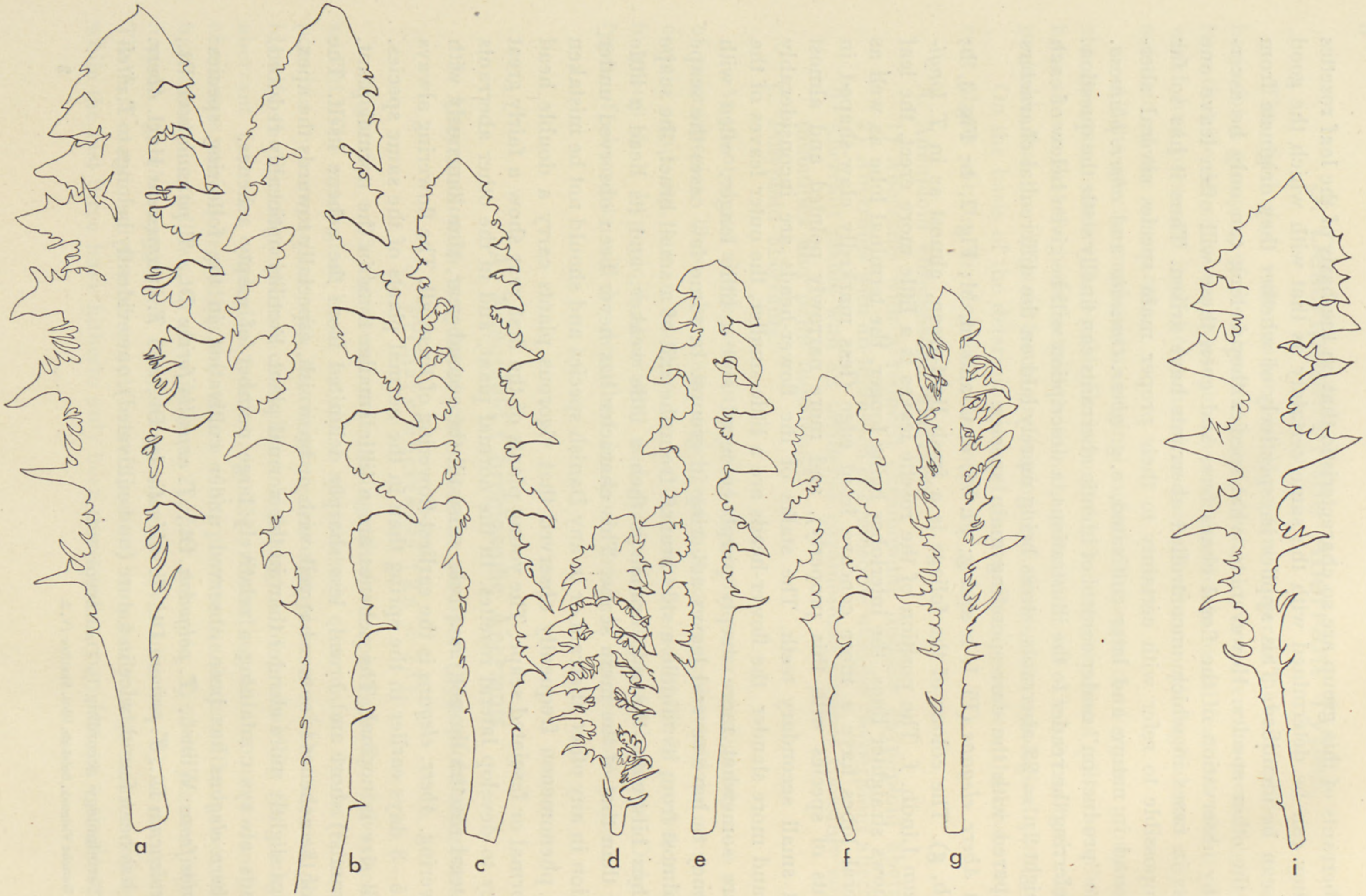

Fig. 2. Summer leaves (about July 1st) of *Taraxacum laciniosifrons* Wiinst. and its 2n = 23 aberrants. a: normal plant; b: *Aberr. elegans*; c: *Aberr. truncata*; d: *Aberr. plumosa*; e: *Aberr. hamosa*; f: *Aberr. pygmaea*; g: *Aberr. tenuis*; i: *Aberr. crassifolia*. $^1/_2$ natural size. del. G. Guðjónsson.

Fig. 3. Summer leaves (about July 1st) of *Taraxacum polyodon* Dt. and its 2 n = 23 aberrants. a: normal plant; b: *Aberr. elegans*; c: *Aberr. truncata*; d: *Aberr. plumosa*; e: *Aberr. hamosa*; f: *Aberr. pygmaea*; g: *Aber. tenuis*; h: *Aberr. olivacea*, i: *Aberr. crassifolia*. ($^1/_2$). del. G. Guðjónsson.

liniforme Hagl., the other is, no doubt, a segregation of *T. floribundum n. sp. ad interim* (a species not yet identified, which is of common occurrence around Copenhagen).

2) *Aberr. truncata* (Pl. I, c, h; Pl. VI, d, D and n, N; Fig. 2, c; Fig. 3, c; Fig. 4, c, h). Colour of leaves somewhat yellowish-green. Leaves relatively short, with a broad lamina. Weaker plants show a tendency to form entire leaves with close-set, somewhat irregular teeth. Vigorous plants have, indeed, incised leaves with numerous close-set patent short lobes, but the indentations often extend only halfway to the main nerve, and actual interlobes are not found. The terminal section is small and often poorly delimited. Stalks of flower-heads long and slender, hence they are as a rule not erect on maturation of the fruit but more or less prostrate or ascending. Scapes of a somewhat reddish colour. Flower-heads large, with densely crowded florets, distinctly more arched than in the main species and of a remarkably dark yellow or nearly orange colour. Bud of flower-head before expansion very short and broad, truncate, often more or less open during the whole development. The bracts of the involucre, as it were, not long enough to enclose the whole bud. External involucre mostly somewhat tousled, its leaves being irregularly bulged. The flowering

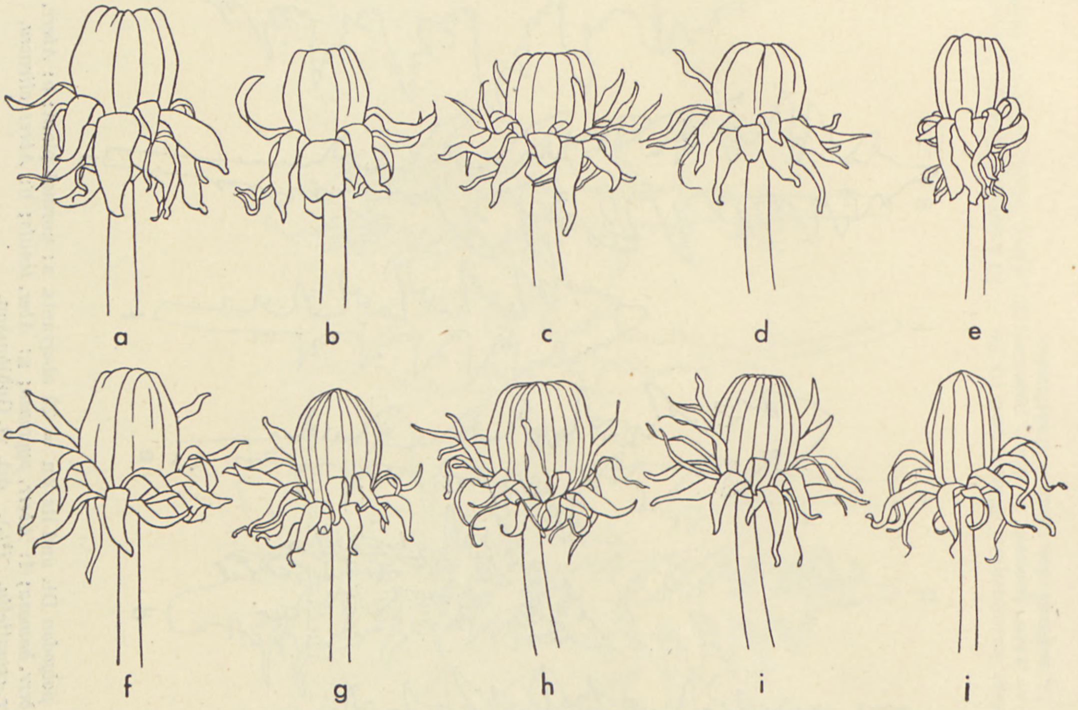

Fig. 4. Heads, immediately before expansion, of *Taraxacum laciniosifrons* Wiinst. and *Taraxacum polyodon* Dt. with 2 n = 23 aberrants.
a—e: *T. laciniosifrons*; f—j: *T. polyodon*: a, f: normal plants; b, g: *Aberr. elegans*; c, h: *Aberr. truncata*; d, i: *Aberr. plumosa*; e, j: *Aberr. hamosa*. Size $^{1}/_{1}$. del. Ingeborg Frederiksen.

sets in about three or four days later than in the corresponding normal plants. Achenes a little smaller than in the normal, pyramis broad, indistinctly marked, rostrum longer than in the normal plant. Colour of achenes deep brownish.

This aberrant shows some tendency to collapse during the flowering, giving rise to "gaps" in the rows. However, a regeneration takes place from the root, the rows being complete again in the late summer. The development and maturation of the fruit are remarkably slow. The time that elapses from the flowering to the ripening of the fruit is always much longer in *aberr. truncata* than in the normal plants or in any of the other aberrants. The fertility is somewhat reduced, a great many empty or poorly developed achenes being always present. The seed germinates slowly. Seedlings with only one cotyledon are of frequent occurrence, and other cotyledonous abnormalities have likewise been observed. Size of cell normal.

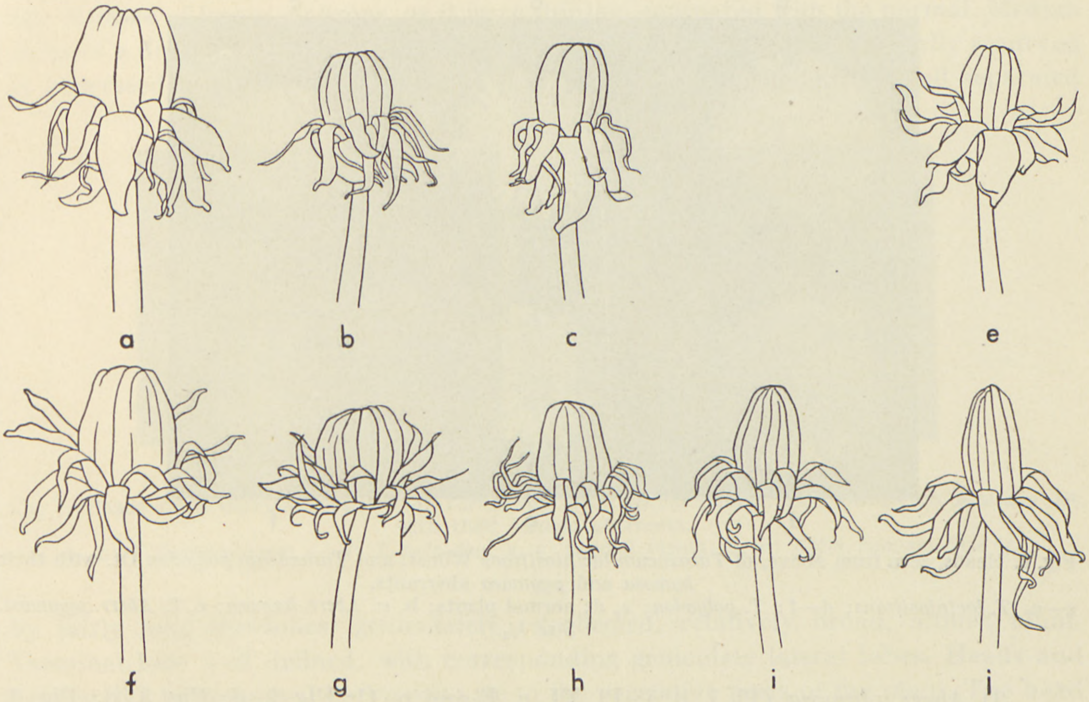

Fig. 5. Heads, immediately before expansion, of *Taraxacum laciniosifrons* Wiinst. and *Taraxacum polyodon* Dt. with 2 n = 23 aberrants.
a—e: *T. laciniosifrons*; f—j *T. polyodon*; a, f: normal plants; b, g: *Aberr. pygmaea*; c, h: *Aberr. tenuis*; i: *Aberr. olivacea*; e, f: *Aberr. crassifolia*. Size $^1/_1$. del. Ingeborg Frederiksen.

Under cultivation *aberr. truncata* has arisen from the following species: *T. laciniosifrons* Wiinst., *T. polyodon* Dt., *T. expallidiforme* Dt., *T. pannulatum* Dt., *T. chloroleucum* Dt., *T. privum* Dt., *T. sublaeticolor* Dt., *T. obliquilobum* Dt., *T. Dahlstedtii* Lindb. f., *T. Arrhenii* Palmgr., *T. floribundum n. sp. ad interim*. In nature, where *aberr. truncata* is recognisable even at a distance on account of its strongly arched deep yellow flower-heads, four *truncata* plants have been found. Two of these, which were later cultivated in progenies for a number of years, possibly originate from *T. dilatatum* Lindb. f. and *T. pallescens* Dt. respectively. However, the safe identification is not possible at all until *aberr. truncata* has been produced from the particular species for direct comparison.

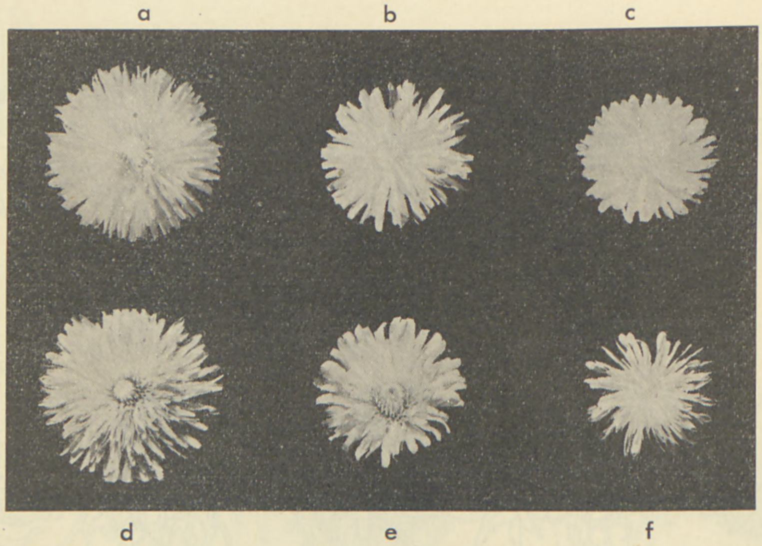

Fig. 6. Heads, seen from above, of *Taraxacum laciniosifrons* Wiinst. and *Taraxacum polyodon* Dt. with their *hamosa* and *pygmaea* aberrants.
a—c: *T. laciniosifrons*; d—f: *T. polyodon*; a, d: normal plants; b, e: *Aberr. hamosa*; c, f: *Aberr. pygmaea.* Size $^1/_2$.

3) *Aberr. plumosa* (Pl. I, d, i; Pl. VI, e, E and o, O; Fig. 2, d; Fig. 3, d; Fig. 4, d, i). Foliage of a dull, deep, dark green colour. Leaves short, erect at the ground, then bent convexly outward, the apex often reaching the surface of the ground. Lobes numerous, very close-set, with a long narrow point, highly claw-shaped retroflected and provided with numerous small acute teeth of the second order. Incisions deep, almost reaching the median nerve. Leaves as a whole somewhat crispate. Stalks of flower-heads rather short, erect. Buds of flower-heads short. Bracts of external involucre a little longer and narrower and more spreading than in the normal plant. Ligules narrow, outer ones relatively long and radiating, so that the head seems to be fairly spare-flowered. Flowering 3—4 days later than the corresponding main species. Achenes of about the same length as in the normal plants, comparatively broad, towards the apex with a few, but strong spicules. Pyramis short, or extremely short, sometimes almost lacking. Colour slightly darker than in the normal. Seedlings with remarkably narrow, relatively long cotyledons. Cell size a little smaller than in the main species. Fertility good.

Under cultivation *aberr. plumosa* has arisen from the following species: *T. laciniosifrons* Wiinst., *T. polyodon* Dt., *T. expallidiforme* Dt., *T. pannulatum* Dt., *T. chloroleucum* Dt., *T. sublaeticolor* Dt., *T. tenebricans* Dt.

Aberr. plumosa, probably belonging to *T. intricatum* Lindb. f., has been found once in nature (and cultivated).

4) *Aberr. hamosa* (Pl. I, e, j; Pl. VI, f, F and p, P; Fig. 2, e; Fig. 3, e; Fig. 4, e, j). Slender and smaller than the respective main species. Foliage with a faint steel-bluish tint. Surface of leaves glabrous, as it were shining, compared with the normal. Median nerve of a distinctly stronger colour. Radical leaves more or less horizontally recurved or adpressed to the substratum. Leaf form very characteristic. Lobes well separated by fairly long interlobes, geniculately retroflected, relatively broad, almost blunt. Terminal lobe well defined, with corresponding geniculate lateral lobes. Heads and head stalks harmoniously proportionate to the vegetative parts of the plant. The head itself is very characteristic: ligules relatively broad, distinctly curved upward and outward, which gives a graceful appearance to the head (Fig. 6, b, e). The heads close much later in the evening than in the corresponding main species, and probably on account of the outwardly curved position of the ligules, the heads are only half closed in the dormant position, not, as normally, closely constricted at the apex (Fig. 7). Outer involucre much reflexed, its bracts tapering into a very long, slender, often twisted point. Flowering period the usual one or a little earlier than in the normal plant. Achenes very small, relatively short, broad, with a sharply delimited, fairly long pyramis. Their scale covering and spicules more scanty, almost restricted to the upper part, colour as in the main species. Roots remarkably long and sparsely branched as can be distinctly observed when the plants are transplanted from the flat boxes to the open ground; an exceptionally small quantity of soil adheres to the roots of the plants. After the flowering and ripening of the fruits in the second or third year a larger or smaller number of the plants will die without any previous symptoms of

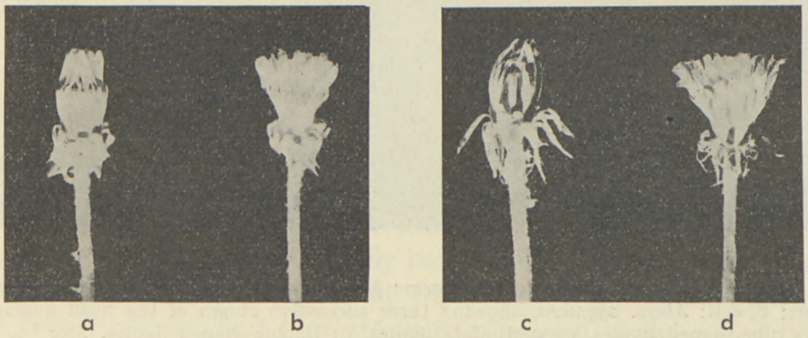

Fig. 7. Heads in a dormant position of *Taraxacum laciniosifrons* Wiinst. and *Taraxacum polyodon* Dt. with their *hamosa* aberrants.
a—b: *T. laciniosifrons*; c—d: *T. polyodon*; a, c: normal plants; b, d: *Aberr. hamosa*. Size $^1/_2$.

weakness. Seedlings small, cotyledons relatively much narrower than in the main species. Cell size normal.

Under cultivation *aberr. hamosa* has been segregated from the following species: *T. laciniosifrons* Wiinst., *T. polyodon* Dt., *T. expallidiforme* Dt., *T. chloroleucum* Dt., *T. sublaeticolor* Dt., *T. cordatum* Palmgr.

Spontaneous specimens of this aberrant have not hitherto been observed in nature.

5) *Aberr. pygmaea* (Pl. II, b, g; Pl. VI, g, G and q, Q; Fig. 2, f; Fig. 3, f; Fig. 5, b, g). Small, but vigorous plant, stout and robust of stature. Colour of foliage normal. In the leaves, when the plant is flowering, the lobes are often numerous, acute, and slightly reflected. In the late summer, outside the flowering period, it shows a great tendency to produce entire blunt leaves with a slightly toothed margin or with only a few pairs of lobes and a large terminal section. Scapes of flower-heads short and stout. Buds of heads short and broad. Outer involucral bracts narrow, tapering to a point even from the base, less recurved than in the normal plant. Heads relatively many-flowered with short ligules, which gives to them a close, compact appearance (Fig. 6, c). On the opening of the head the ligules are more or less tubularly rolled up with margins connate. They soon split from the apex, appearing spathulate (Fig. 6, f). The splitting then takes place rather rapidly towards the base, the typical ligular corolla being thus realised. The tendency to develop tubular corollas is somewhat different in the various species. The most characteristic tubular corollas can be observed in *aberr. pygmaea* of *T. bracteatum* (Fig. 8, b, c, d) and *T. pannulatum*, in which whole heads one or two days after the expansion have only tubular corollas, which gives the flowering plant a very peculiar appearance. In *T. laciniosifrons* and *T. polyodon* the splitting of the marginal corollas as a rule takes place before the whole head is expanded. In all *pygmaea* aberrants the marginal ligules are of a deep purple colour on their outer side (as in *T. speciosum* Raunk.). Flowering time as in the normal plant or slightly earlier. Achene relatively large, fusiform, the whole

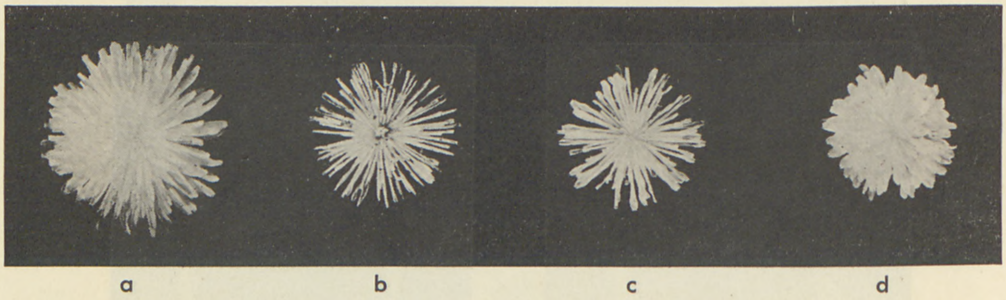

Fig. 8. Heads, seen from above, of *Taraxacum bracteatum* Dt. and its *pygmaea* aberrant. a: normal plant; b, c, d: *Aberr. pygmaea,* showing three successive stages of the head during expansion. b: tube-shaped ligules, c: spathulate ligules, d: tongue-shaped ligules. Size $^1/_2$.

surface densely covered with spicules, tapering in the pyramis. The latter broad and not separated from the achene itself, the spicules continuing right to the colourless rostrum, the lower part of which is broad and more or less compressed. Rostrum otherwise remarkably short and stout. Colour of achene appreciably brownish-yellow as compared with that of the normal plant. Cotyledons small and thick, rather often double, one, or both of them, being split to the base. Cell size normal.

The root system differs from that of the normal plant. The main roots are short, but exceedingly much branched. On planting from the flat boxes it will always be noticed that the soil adheres to the roots to an exceptional degree, so that no particular care is required to secure the plants with a lump of soil.

Under cultivation *aberr. pygmaea* has been ascertained in the following species: *T. laciniosifrons* Wiinst., *T. polyodon* Dt., *T. pannulatum* Dt., *T. expallidiforme* Dt., *T. sublaeticolor* Dt., *T. subcyanolepis* M. P. Chr., *T. cordatum* Palmgr., *T. obliquilobum* Dt., *T. bracteatum* Dt., *T. hamatum* Raunk.

6) *Aberr. tenuis* (Pl. II, c, h; Pl. VI, h, H and r, R; Fig. 2, g; Fig. 3, g; Fig. 5, c, h). Small plant of slender stature; the latter character is seen to a greater extent in the stalks of the flower-heads and the heads than in the leaf rosettes. Colour of foliage normal. Leaves highly different in shape from those of the normal plant. They are relatively long, narrow, with a particularly large number of narrow and blunt patent lobes, the terminal one indistinctly marked. Often the leaves are somewhat groove-like concave. In their proximal part they are flatly adpressed to the soil, in their distal end ascending, the whole leaf rosette being thus flatly cup-shaped (vigorous rosettes). Stalks of flower-heads very slender, relatively long, often ascending. Flower head small, bud of flower-head narrow. Outer involucral bracts long and broad in relation to the size of the head. Ligules thin, being accordingly more or less transparent as compared with those of the normal plant, which lends to the head as a whole a rather dilutedly yellow colour. The ligules show a marked tendency to turn sidewards, with the edges directed upwards, the whole flower-head being accordingly of a characteristic turbinate shape (Fig. 9). Flowers 8—10 days later than the normal plant. Achenes small and narrow, with a small number of spicules near the apex. Pyramis long, well defined. Colour rather faint, brownish towards the apex. Seedlings slender. Cell size much smaller than in the normal plant.

The fertility in *aberr. tenuis* is very inconsiderable, but seems to vary from plant to plant, and the heads of the same plant likewise often differ greatly as regards fertility. In the progeny of primary aberrants, in so far it has hitherto been possible to produce such, a number of the plants seem to be entirely sterile. In most of them the greater part of the heads is sterile, while some few heads have now and then developed some achenes.

In spite of the slender stature of the plant its durability as compared with that of the normal plant is hardly reduced. Older plants possess a disproportionately vigorous and durable root system, a thick tap-root with a branched mesocorm and an exceedingly large number of rosettes.

Under cultivation *aberr. tenuis* has so far only been observed in three species, viz. *T. laciniosifrons* Wiinst., *T. polyodon* Dt., and *T. cordatum* Palmgr.

7) *Aberr. olivacea* (Pl. II, i; Pl. VI, s, S; Fig. 3, h; Fig. 5, i). The colour of the foliage is the most conspicuous difference from the normal plant. The leaves are of a peculiar yellowish-greeno r olive-green colour, which is not always equally distributed over the whole leaf. Otherwise it differs little from the normal. Its growth is a little more slender, the lobes of the leaves slightly more curved, and the terminal section often larger and more blunt. The heads are altogether more slender. Outer involucral bracts of a deeper colour, colour of flowers inconsiderably lighter than in the normal plant. Achenes almost as in the normal plant, slightly smaller and with a little shorter rostrum. Cell size normal. Fertility rather good.

This aberrant has hitherto only been observed in *T. polyodon* Dt., in which, on the other hand, it is of fairly frequent occurrence.

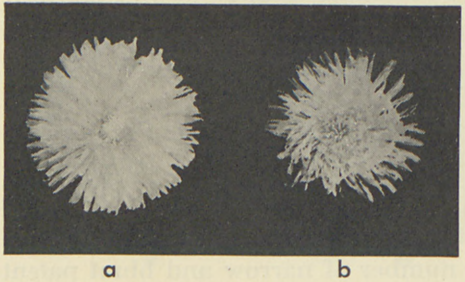

Fig. 9. Heads, seen from above, of *Taraxacum laciniosifrons* Wiinst. and its *tenuis* aberrant. a: normal plant: b: *Aberr. tenuis* (note its turbinate head). Size $^1/_2$.

8) *Aberr. crassifolia* (Pl. II, e, j; Pl. VI, j, J and t, T; Fig. 2, i; Fig. 3, i; Fig. 5, e, j). The plant is smaller than the normal plant. Leaves rather thick, erect, with fairly acute, somewhat patent, close-set lobes. Terminal section large, triangular, not sharply delimited. Scapes of heads slender. Heads rather small, with a disproportionately large outer involucre. Achenes of the same size as in the normal plant or sometimes a little larger, chiefly with strong spicules towards the apex. Pyramis rather broad, less sharply delimited, and rostrum a little shorter than in the normal plant. Fertility good.

Aberr. crassifolia has so far only been noted in *T. laciniosifrons* Wiinst., and *T. polyodon* Dt. It is the aberrant which is most difficult to recognise, and it may possibly have been overlooked in the first experimental series. For in a vegetative state it may resemble *aberr. gigas* rather much (see below p. 20), so vigorous plants may be mistaken for polyploids.

Since only the *polyodon* aberrant of this type has been cultivated in generations of progeny, our knowledge of this aberrant at the present time must be said to be rather imperfect. There is hardly any doubt, however, that it belongs to the least frequent 2 n = 23 aberrants.

b. Secondary aberrants (2n = 22).

The hereditary conditions in the aberrants have been most extensively studied in *T. laciniosifrons* and *T. polyodon*. In seed progenies of the primary aberrant plants the particular aberrant type will be obtained in the first generation of progeny as well as in the following generations, as might be expected. But as in the main species, a segregation of new aberrants takes place, often in a much larger number than in the original species. The conditions of segregation in the aberrants of the 2 n = 23 series entirely resemble those in the main species, as described above. The aberrants of the second order (secondary aberrants) form parallel series to the primary aberrants but are never identic with any of these latter. Thus, for instance, *aberr. elegans* segregates the secondary aberrants *truncata, plumosa, hamosa,* and *tenuis.* All these secondary aberrants to a certain extent retain the *elegans* characters, for instance the light green colour of the leaves and the fairly long distance between the lobes, combined with the characters of the respective aberrant types (cf. Pl. 4). In the following pages these secondary aberrants will be designated e. g. as follows: *aberr. elegans* → *truncata, aberr. elegans* → *plumosa,* etc. All secondary aberrants are weaker than the two primary types of which they are composed, and the fertility is, as a rule, reduced. The secondary aberrants of this series have the chromosome number 2 n = 22. Accordingly they have lost one more chromosome. Thus, for instance, *aberr. elegans* → *plumosa* lacks the two chromosomes which have been lost in the primary aberrants *aberr. elegans* and *aberr. plumosa,* respectively.

The frequency of segregation, which will be illustrated numerically below, varies greatly within the different types of aberrants. Thus *aberr. elegans,* which is the most highly segregating of the primary aberrants, yields about ten times as many aberrants as the main species, while *aberr. truncata* does not show a much more frequent segregation than the normal plants.

c. Tertiary aberrants (2 n = 21).

The secondary aberrants may, in turn, segregate tertiary aberrants. These are, as a rule, much weaker and little capable of surviving, and it may therefore sometimes be difficult to refer them definitely to certain aberrant types. However, that tertiary aberrants form parallel series to the secondary and primary aberrants, is beyond doubt. Specimens investigated cytologically had the chromosome number 2 n = 21. Two tertiary *laciniosifrons* aberrants, judging from the leaf form rather *plumosa* types as compared with the parent plants, both *elegans* → *hamosa,* however, had only 2 n = 20 and 2 n = 19. The last-mentioned figure is the lowest figure so far observed in any aberrant. The parent plants, both with the chromosome number 2 n = 22, of these two aberrants are derived from two different primary *elegans* segregations. In other cases, also, the simultaneous loss of two chromosomes in tertiary aberrants was ascertained. Whether there is actually an increasing tendency to lose several chromosomes at the same time within the higher links of this series of hypoploid aberrants, it is impossible to decide. At any rate corresponding cases have not been ascertained in primary aberrants.

2. Aberrants with an increased chromosome number (hyperploid aberrants).

As stated above, by far the majority of aneuploid aberrants can be immediately referred to one or the other of the primary aberrant types with the chromosome number $2n = 23$.

However, the numbers $2n = 25$ and $2n = 26$ have occasionally been ascertained in, so to speak, sporadically occurring aberrants, which may probably be just as easily recognisable as aberrants of the $2n = 23$ types, but which according to their morphological characters cannot be referred to any of them.

Such aberrants will not be dealt with at length in the present paper, neither morphologically nor cytologically.

B. Aberrant Plants with unaltered Chromosome Numbers.

It might be natural to assume that the appearance of forms differing morphologically will always be associated with, or depend on, a chromosome aberration. The cytological investigation of a number of more rarely occurring aberrant plants revealed, as stated above, some few cases of an increased chromosome number. More frequently, however, the chromosome number $2n = 24$, as in the normal plant, was found. Such plants with an unaltered chromosome number may in certain cases be just as morphologically different from the normal plant as the $2n = 23$ aberrants. Hitherto it has not been possible to ascertain types of this group analogous to the different species. The idiograms for these aberrants have not yet been made the subject of closer study.

C. Polyploid Aberrants.

In seed progenies of both normal plants and aberrants belonging to the $2n = 23$ series such aberrants will arise, in addition to those mentioned above, as immediately suggest polyploids. The polyploid nature of such plants was confirmed by the cytological investigations, which showed that they have a doubled chromosome number. Aberrants with a doubled chromosome number will be designated *aberr. gigas* on the analogy of the $2n = 23$ aberrants.

Aberr. gigas ($2n = 48$). (Pl. III, b, d; Pl. VI, a, A and k, K; Fig. 10, b, d; Fig. 11, b, d). By its external morphological characters alone this aberrant appears as a distinct *gigas*-form, though in such a way that the specific characters have been obliterated in an appreciable degree. The whole plant is to a certain extent disproportionate, the flower heads being disproportionately large as compared with the leaf rosette. The leaves are thick and more erect than in the normal plant. The shape of the leaf differs greatly from the normal. The spring leaves in vigorous plants are as a rule deeply and irregularly incised. Undivided leaves, often finely toothed at the margin, are very frequent later in the summer. The leaf is shorter than in the normal plant, while the breadth is often comparatively great. The leaves are often irregularly twisted. Owing to these characters *aberr. gigas* of different species often present such a great resemblance to each other that they can hardly be distinguished by the shape of their leaves. The characteristic features of the species are somewhat

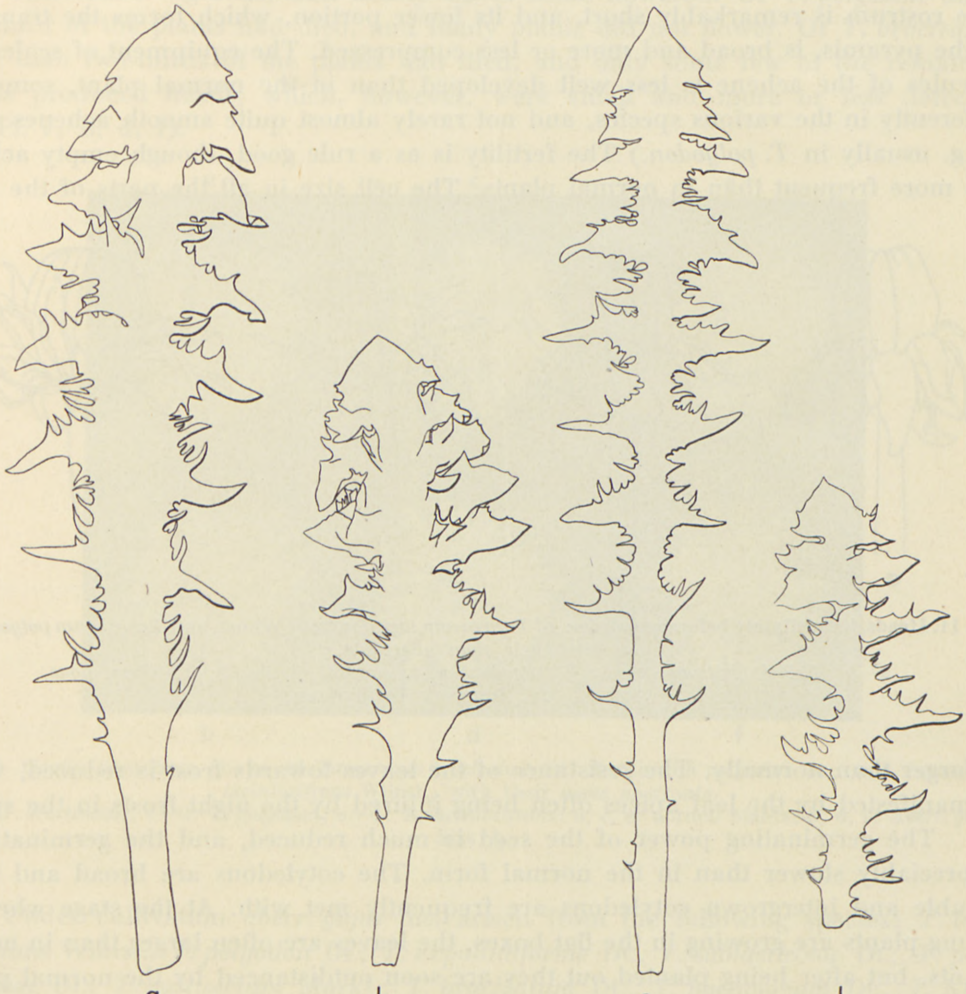

Fig. 10. Summer leaves (from about July 1st) of *Taraxacum laciniosifrons* Wiinst. and *Taraxacum polyodon* Dt. with their *gigas* aberrants.
a—b: *T. laciniosifrons*; c—d: *T. polyodon*; a, c: normal plants; b, d: *Aberr. gigas.*
Size $^1/_2$. del. G. Guðjónsson.

better preserved in the floral characters. A common feature of all *gigas* aberrants is, however, that the scape of the head is stiffly erect and with the strengthening tissue so poorly developed that it will readily be broken by the wind or other superficial injury. The bud of the head is broad and relatively short. The head is altogether larger, the ligules broader, often conspicuously toothed, and the sequence of opening of the individual florets in the head is often more irregular than in the normal plant (Fig. 12, b, d, f). The fruits are much larger and of a different shape. The achene proper is not distinctly separated from the pyramis, which is very broad and stout. The rostrum is remarkably short, and its lower portion, which forms the transition to the pyramis, is broad and more or less compressed. The equipment of scales and spicules of the achene is less well developed than in the normal plant, somewhat differently in the various species, and not rarely almost quite smooth achenes occur (e. g. usually in *T. polyodon.*) The fertility is as a rule good, though empty achenes are more frequent than in normal plants. The cell size in all the parts of the plant is larger than normally. The resistance of the leaves towards frost is reduced, which is manifested by the leaf apices often being injured by the night frosts in the spring.

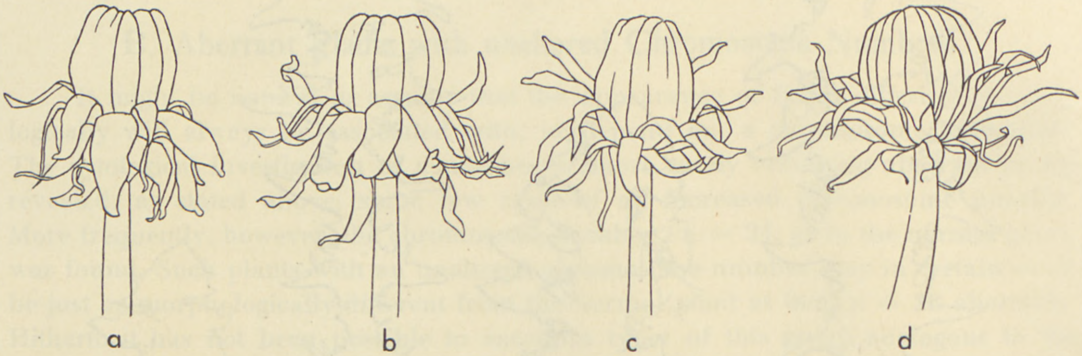

Fig. 11. Heads, immediately before expansion, of *Taraxacum laciniosifrons* Wiinst. and *Taraxacum polyodon* Dt. with their *gigas* aberrants.
a—b: *T. laciniosifrons*; c—d: *T. polyodon*; a, c: normal plants; b, d: *Aberr. gigas.*
Size $^1/_1$. del. Ingeborg Frederiksen.

The germinating power of the seed is much reduced, and the germination is appreciably slower than in the normal form. The cotyledons are broad and thick. Double and intergrown cotyledons are frequently met with. At the stage when the young plants are growing in the flat boxes, the leaves are often larger than in normal plants, but after being planted out they are soon outdistanced by the normal plants. In the development of the root system *aberr. gigas* differs greatly from the normal, having a very thick main root and a rather slight development of lateral roots. On this account the plants are often damaged by the frost in the winter, the crown of the root being elevated above the surface of the ground. Consequently, but evidently for purely physiological reasons also, the lifetime of the plant is much reduced. In the first year of flowering the plants still look sound and vigorous. The two-year plants are appreciably weakened, and the three-year plants are often so much weakened that many of them do not even flower, and a number of them die. Curiously enough, it is evidently not all species that tolerate the doubling of the chromosomes equally well. *Aberr. gigas* of the three species *T. laciniosifrons* Wiinst., *T. polyodon* Dt., and *T. bracteatum* Dt., which was for some years cultivated on a large scale, showed this with remarkable distinctness: in three-year old cultures of *T. laciniosifrons* the plants were still rather vigorous, and nearly all of them flowered. Of *T. polyodon* about one-third of the plants had died, and many plants did not flower. Of *T. bracteatum* more than two-thirds of the plants had died, and only some few of the remaining plants produced heads, which, however, were small and more or less defective (cf. Pl. V, b, d, f).

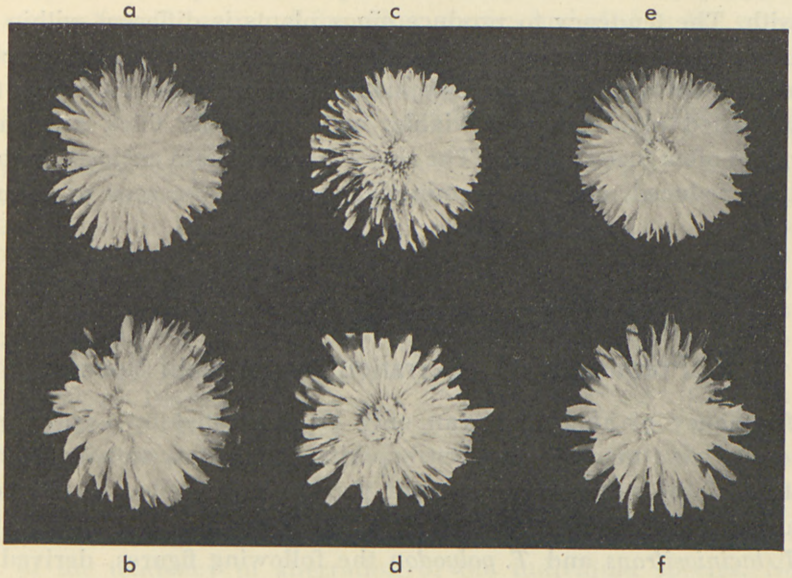

Fig. 12. Heads, seen from above, of *Taraxacum bracteatum* Dt. *Taraxacum polyodon* Dt., and *Taraxacum laciniosifrons* Wiinst., with their *gigas* aberrants.
a—b: *T. bracteatum*; c—d: *T. polyodon*; e—f: *T. laciniosifrons*; a, c, e: normal plants; b, d, f: *Aberr. gigas.* Size $^1/_2$.

Under cultivation *aberr. gigas* has arisen from the following species: *T. laciniosifrons* Wiinst., *T. polyodon* Dt., *T. expallidiforme* Dt., *T. sublaeticolor* Dt., *T. pannulatum* Dt., *T. vastisectum* Markl., *T. bracteatum* Dt., *T. pycnolobum* Dt., *T. Kjellmani* Dt., *T. obliquilobum* Dt.

In nature *aberr. gigas* of *T. Arrhenii* Palmgr. and *T. acutifidum* M. P. Chr. have been found.

Aberrations in polyploid plants. Of the *gigas* aberrants *T. laciniosifrons, T. polyodon,* and *T. bracteatum,* as stated above, have been cultivated in large numbers. In *T. bracteatum gigas* hardly any variation could be ascertained, while aberrant plants were observed in the two first-mentioned species, but they are more difficult to recognise here than in the 2n = 23 series. An aberrant plant in *T. laciniosifrons gigas* with a somewhat more slender stature and more deeply incised leaves than the ordinary *gigas* had $2n = 46$. In *T. polyodon gigas* there sometimes occur forms with a little larger, lighter-coloured leaves, still larger heads with a more strongly coloured outer involucre and even larger achenes than the ordinary *gigas* plant. A specimen of this type examined cytologically had the chromosome number $2n = 45$.

The polyploids of the aneuploid aberrants. *Gigas* plants are often met with in cultures of $2n = 23$ and $2n = 22$ aberrants. They arise by a simple doubling of the chromosome equipment present and thus have $2n = 46$ or $2n = 44$ respectively. Morphologically it is often difficult to trace these plants back to the original species, since their vitality is as a rule reduced. However, exceptions in this respect have been met with. The tendency to produce *gigas* plants is different within the various $2n = 23$ aberrants. A *gigas* plant of the above-mentioned category which is of particularly frequent occurrence is *aberr. pygmaea* → *gigas*, a peculiar small thick-leaved and highly twisted plant not very viable, with unusually thick and short achenes which are rather often fused in pairs. The ripe achenes remain enclosed in the involucre. The fertility is reduced, and the germinating power of the seed as a rule poor.

4. Frequency of Aberration.

A. Frequency of Aberration in the main Species.

The frequency of aberration can only be illustrated by approximate figures. No exact counts were made in the first experimental series, and in several series an exact counting of the number of aberrant plants was impeded by severe attacks by wire worms and cockchafer larvæ.

For *T. laciniosifrons* and *T. polyodon* the following figures, derived from carefully controlled series, can be given:

Species	Number of plants	$2n = 23$ aberrants					
		elegans %	truncata %	plumosa %	hamosa %	pygmaea %	tenuis %
T. laciniosifrons	6000	0.1	0.05	0.3	0.1	0.1	0.05
T. polyodon	1650	0.05	0.05	0.1	0.2	0.2	+

	$2n = 23$ aberrants		aberrant plants not belonging to the $2n = 23$ series	total	gigas
	olivacea %	crassifolia %	%	%	%
T. laciniosifrons	—	+	1.4	2.1	0.8
T. polyodon	0.1	+	0.6	1.3	0.8

Whether there is actually any difference in the frequency of segregation between the two species cannot be decided on the basis of the numerical material at hand. The same applies to the frequency of the individual aberrant types in the two species.

Some few points of difference have, however, been demonstrated with certainty; thus *T. laciniosifrons* does not segregate *aberr. olivacea*. This aberrant has hitherto only been observed in *T. polyodon*, where it occurs rather frequently both as a primary aberrant and a secondary aberrant. *Aberr. tenuis* has repeatedly been observed as segregated from *T. laciniosifrons*, both primarily and secondarily (of *aberr. elegans*). In *T. polyodon* it was only observed once as a primary aberrant, but it also occurs as a secondary aberrant, which is shown both by morphological and cytological characteristics.

For comparison with the two species already mentioned the approximate frequency of segregation for some of the other species included in the experiments will be given below:

Species	Number of plants	Total of aberrant plants less *gigas* %	*gigas* %
T. protractifrons Dt.	76	8.0	0
T. expallidiforme Dt.	280	4.2	0.4
T. sublaeticolor Dt.	150	2.6	0.7
T. pannulatum Dt.	300	3.0	0.3
T. privum Dt.	100	2.0	0
T. intumescens Hagl.	206	1.5	0
T. floribundum n. sp.	300	1.3	0
T. subcyanolepis M. P. Chr.	300	0.7	0
T. hamatum Raunk.	200	0.5	0
T. bracteatum Dt.	c. 1000	0.2	0.2
T. copidophyllum Dt.	c. 1000	0.1	0

It is evident that general validity should not be ascribed to these figures as indications of the tendency to aberration of the individual species. No doubt the frequency of aberration will vary from one experiment to the other. Moreover the apparent power of aberration will depend on the care with which the experiments are made. Under less favourable conditions of growth the weakest aberrants will easily die, even during the earliest stages of growth, and thus escape attention. However, that the frequency of aberration differs within the different species, is beyond any doubt. The experiments, which were started with mass planting of *T. copidophyllum*, *T. bracteatum*, and *T. laciniosifrons*, showed this very clearly even in the first experiments. The two first-mentioned species, and notably *T. copidophyllum*, distinguished themselves by a very great constancy compared with *T. laciniosifrons*. The tendency to aberration seems to be a property inherent in the species, even in its aberrants. As will appear from the above table, *T. bracteatum* belongs to the slightly segregating species. Its only aberrants ascertained so far, *aberr. pygmaea* and *aberr. gigas*, have shown a marked constancy in their progeny in contrast to the parallel aberrants of for instance *T. laciniosifrons* and *T. polyodon*.

As will likewise be seen from the table, the highest aberration figure ascertained so far was found in *T. protractifrons*. It is peculiar to the aberrant plants of this species that on a morphological basis none of them can be referred with certainty to the types of the main series 2 n = 23. Three of the most deviating plants, the only ones which have hitherto been investigated cytologically, had the chromosome numbers 2 n = 22, 2 n = 24, and 2 n = 26.

In the other species, highly as well as slightly segregating, the greater number of the aberrant plants belong to the 2 n = 23 types. Thus, for instance, the highly segregating *T. expallidiforme* seems to produce comparatively much fewer "indeterminable" aberrants, that is to say, such as do not belong to the 2 n = 23 series, than *T. laciniosifrons* (cf. the table on p. 24).

B. Frequency of Aberration in the primary Aberrants of the main Series 2 n = 23.

The frequency of aberration in the primary 2 n = 23 aberrants varies in the different types. A few series of aberration figures for primary aberrants of *T. laciniosifrons* and *T. polyodon* will be given below:

Primary aberrant (2 n = 23)	Number of plants	Secondary aberrant plants (mainly 2 n = 22 aberrants) %	*gigas* (2 n = 46) %
T. laciniosifrons aberr. elegans	843	c. 11	2.3
— — *truncata*	787	c. 2	0.2
— — *plumosa*	196	c. 4	0.5
— — *hamosa*	126	c. 3	0.8
— — *pygmaea*	350	c. 4	3.0
T. polyodon — *elegans*	237	c. 11	0.4
— — *truncata*	288	c. 2	2.4
— — *plumosa*	154	c. 4	0.7
— — *hamosa*	369	c. 3	0
— — *pygmaea*	410	c. 3	3.4

It appears from these figures that analogous aberrants in the two species show an approximate agreement in their frequency of aberration as far as secondary aberrants are concerned. The occurrence of *gigas* plants, however, seems to be more casual.

It is clear that *aberr. elegans* yields more aberrants than the other primary aberrants. Analogous *elegans* aberrants of other species, also, have given similar high segregation figures in culture experiments. *T. floribundum aberr. elegans*, found in nature, yielded even c. 25 % of aberrants in its progeny.

In *T. laciniosifrons aberr. elegans* the secondary aberrants *elegans* → *truncata*, *elegans* → *plumosa*, *elegans* → *hamosa*, and *elegans* → *tenuis* are segregated about ten times as frequently as the parallel primary aberrants of the main species. Something similar applies to *T. polyodon aberr. elegans*, in which, however, the secondary *aberr. tenuis* has not hitherto been ascertained. Altogether *aberr. tenuis* occurs much more frequently, both as primary and secondary aberrants, in *T. laciniosifrons* than in *T. polyodon*. The secondary *aberr. olivacea*, however, occurs especially frequently as a segregation of *polyodon aberr. elegans*. The secondary *aberr. pygmaea* has not been found with certainty to have been segregated from *aberr. elegans* or from the other primary aberrants.

The primary aberrants *plumosa*, *hamosa*, and *pygmaea* segregate less than *elegans*, but yet more than the normal plant. It is peculiar to *aberr. pygmaea* that it produces *gigas* plants much more frequently than the other primary aberrants. This applies not only to the two species mentioned in the table, but also to others, thus to a remarkable extent to *T. pannulatum*.

Aberr. truncata is strangely constant. *T. polyodon aberr. truncata* has exceptionally, as shown by the above table, produced a large number of *gigas* plants, but otherwise the frequency of aberration is relatively low. In *T. laciniosifrons aberr. truncata* (progeny cultivated from three primary plants) the tendency to collapse is great, so the records of aberrations are rather uncertain. Progeny of two *truncata* plants found in natural habitats, possibly of *T. pallescens* Dt., and *T. dilatatum* Lindb. f., has proved to be practically constant. *Aberr. tenuis* of *T. laciniosifrons*, which, however, was only cultivated in smaller numbers owing to the poor fructification, seems likewise in a rather slight degree to give rise to secondary aberrants.

5. Discussion.

As regards the causes of the occurrence of the aberrants we can only guess at the present time. The probability of a wholly or partially sexual reproduction is at the outset very small for the species in question. All the *Taraxaca* which have hitherto been found to be sexual have the chromosome number $2n = 16$, while those used in the experiments had $2n = 24$. Accordingly they are triploid. The segregations are moreover of quite another and more radical character than such as might be expected by a simple new combination of genes resulting from fructification and meiosis, if any. So as to include all possibilities agamisation experiments were repeatedly made on the particular plant material by cutting off the uppermost portion of the heads before their opening according to RAUNKIÆR's classical method (RAUNKIÆR 1903). The result was each time that the frequency of aberrants was essentially the same after the sowing of achenes from agamised heads as from intact heads.

It has been shown experimentally that aberrant types can be produced in a purely vegetative way. This has been demonstrated in two ways 1) by the appearance of chimaeric plants, and 2) by the appearance of aberrants in clones produced by reproduction by root cuttings of one and the same plant.

The author regards it as most probable that the most frequent of all aberrants, viz. the polyploid aberrants, mainly arise by abnormalities in the somatic tissues. For *gigas* sectorial chimaeras are of frequent occurrence. Especially among the young plants rosettes with a larger or smaller sector of *gigas* characters are not rarely met with. With increasing age such plants often become normal, the normal tissue owing to its more intense growth sooner or latter conquering the whole growth point. Sometimes, however, the chimaeric character will persist until the flowering time, the plant thus producing both normal and *gigas* heads. In addition, root cuttings of apparently non-chimaeric *gigas* aberrants have in many cases yielded normal individuals, which shows that at any rate part of the root has not participated in the aberration. A *gigas* plant found in a natural habitat in 1943 likewise produced normal plants of root cuttings, but *gigas* plants by seed reproduction. Other, non-polyploid, aberrant plants have also arisen as chimaeras, and this applies both to such as have preserved the chromosome number unaltered and such as have an altered (increased) chromosome number.

That a vegetative formation of aberrant plants by root cutting reproduction of normal plants can take place, was shown by an experiment with *T. pannulatum*. Of an old and very large plant a clone of c. 300 individuals was produced by root cutting reproduction. Among them there were three different aberrant plants, all of which, however, had an unaltered chromosome number, $2n = 24$. As in the aberrants arisen from seeds, the aberrant characters are transmitted to the progeny, though secondary aberrants will arise now and then.

In this connection it is noteworthy that aneuploid aberrants of the main series $2n = 23$ have not yet been found to have arisen as chimaeras. Numerous plantings of root cuttings of aberrants of this series have not resulted in plants which differed from the primary shoot. In case they should have arisen by alteration of the hereditary conditions in the somatic tissues, we might expect sometimes to come across chimaeric plants which would be able to regenerate from the root individuals of the type of the original mother species. It must therefore be assumed that the appearance of a great many aberrants, especially $2n = 23$ aberrants, is due to irregularities of the meiosos, commenced but not completed, which precedes the formation of the embryo sac.

From the experimental results recorded above it would appear that the series $2n = 23$ occupies a special position, genetically as well as cytologically. This series, together with the polyploid aberrants, comprises the regularly, as it were law-directed, occurring aberrants as compared with the more rarely, apparently casually, appearing aberrants with increased or unaltered chromosome numbers.

In the present work attention has therefore principally been directed towards aberrants of the types $2n = 23$ and $2n = 48$, and the subjoined cytological section is chiefly limited to the establishment of the chromosome numbers and the idiograms of these aberrants.

Continued experimental and cytological investigations for the elucidation of the causes of the aberration phenomena will be dealt with in a later paper.

II. CYTOLOGY

BY

GUÐNI GUÐJÓNSSON

1. Introduction.

Much difficulty is met with in cytological studies of the *Taraxaca*. The root-tips do not fix and stain well in most fluids and stains, the somatic chromosomes are very small, and the meiotic division of the pollen mother cells and embryo sac mother cells of the apomictic species is highly irregular. Earlier authors have therefore been somewhat uncertain as regards the chromosome number. It was first determined with certainty in sexual species, in which the number is low and the meiotic division regular. Thus ROSENBERG (1909) and OSAWA (1913) found the chromosome number of *T. confertum* Dt. and *T. platycarpum* Dt., respectively, to be 2 n = 16.[1]

As regards the apomictic species, the statements were more uncertain (cf. ROSENBERG 1909, OSAWA 1913, HEITZ 1926). ROSENBERG (l. c. p. 160) gives the numbers n = 12—13 and 2 n = 20—30. A similar uncertainty is expressed by HEITZ (l. c., p. 633): "Meistens werden 23—24, ganz vereinzelt auch 22 und 26 Chromosomen gezählt. Ich sage ausdrücklich gezählt, denn diese scheinbare Variation hängt hier sicher mit der erschwerten Beobachtung zusammen." GUSTAFSSON (1932) was the first to ascertain definitely that many apomictic species of *Taraxacum* have 2 n = 24, others 2 n = 32 or 2 n = 40; later (1933) he reported also 2 n = 48. Thus the basic number within the genus *Taraxacum* is 8. Later determinations of chromosome numbers for an additional number of species, made by PODDUBNAJA-ARNOLDI & DIANOVA (1935) and ERLANDSSON (1939), likewise all show multiples of 8. The main result of the cytological investigations of *Taraxacum*-species available so far may be summarised in the statement that all sexual species hitherto examined are diploid, 2 n = 16, while the apomictic species are polyploid.

As mentioned in the first part of this paper, Dr. THORVALD SØRENSEN has, by cultivation experiments, succeeded in demonstrating a number of different aberrant types. The aberrant plants have in some cases been found as deviating individuals in the progeny of the individual normal plants, in others chimaeric plants with

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[1] On the following pages the somatic number is designated 2 n.

sectors of aberrant tissue were found. — This material forms the basis of the cytological studies reported here. In the present paper only the mitotic chromosomes of the root tips will be described. The studies made of P. M. C.s and E. M. C.s will be recorded in a later paper.

As mentioned above it is difficult to obtain a good fixing and staining of the *Taraxacum*-chromosomes; but after trying and comparing a number of fixing and staining methods, I decided to employ one of the first combinations tried, Lewitsky's fixation and Newton's gentian violet method, since with selected root tips, well cared for, this gives the most distinct pictures, especially as regards the position and number of the constrictions. The slides have to be stained for 1—2 hours.

2. The Idiogram of the Normal Plants.

The *Taraxacum*-species which have formed the basis of the experiments dealt with in the present paper are apomicts belonging to the *Vulgaria* group and with the chromosome number 2 n = 24. However, a few diploid sexual forms are found within this group also. Thus Gustafsson (1937) ascertained sexual reproduction in *T. obtusilobum* Dt. and determined the chromosome number of this species as 2 n = 16. In a material resulting from seeds received from Switzerland, M. P. Christiansen (1942 b) found a sexual form also. Gustafsson and M. P. Christiansen kindly placed seeds of their sexual plants at our disposal, and it has thus been possible to include them in the present investigation for comparison with the apomictic species. Gustafsson's record, 2 n = 16 of T. *obtusilobum,* was confirmed by the present writer. Christiansen's sexual Swiss species likewise proved to be diploid (2 n = 16).

With these diploid species as the starting point an attempt was made to determine the idiogram of *Taraxacum*, especially of the *Vulgaria* group. The low chromosome number of the sexual species should here present an advantage over the triploid apomicts. A certain difference in size between the chromosomes has been noted by earlier authors, though they have not followed up the matter in detail. Thus Gustafsson (1932, p. 58) says: "Wegen der allmählichen Übergänge in der Grösse der Chromosomen ist ein deutlicher Unterschied nur ausnahmsweise vorhanden . . .". And he goes on to say: "In wenigen vereinzelten Fällen sind doch qualitative Unterschiede wahrgenommen worden, am leichtesten natürlich in den diploiden Arten." Poddubnaja Arnoldi & Dianova (1934, p. 32) say: "In den somatischen Wurzelzellen aller dieser Arten[1]) sind die Chromosomen dünn, lang, ihre Individualität ist kaum ausgeprägt; von den Chromosomen anderer *Taraxacum*-Arten, sowie auch *Taraxacum kok-saghys* sind sie kaum abweichend. Bei *Taraxacum hybernum* haben wir in manchen Fällen Platten mit etwas kürzeren Chromosomen gesehen (Abb. 21)". And on p. 20 they say: ". . . konnten wir das Vorhandensein eines Chromosompaares mit Trabanten feststellen."

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[1] i. e. *T. laevigatum* (Willd.) DC., *T. officinale* Wigg., *T. parnassicum* DC., *T. hibernum* Dt., *T. retroflexum* N. Lindl., *T. robustum* Schischk., *T. microspermum* Schischk., *T. montanum* (C. A. M.) DC.

Apart from ascertaining the relative size of the chromosomes it is also of importance to elucidate their morphology, that is to say, the position of the primary and secondary constrictions, the occurrence of satellites, etc. The constrictions are most distinct during a short period late in the metaphase. The chromosomes are then somewhat longer and thinner than at the climax of the metaphase, but on the other hand the splitting has then commenced, which may render observation difficult. The chromosomes are often curved with one end projecting outside the plane as indicated in the drawings. This feature in connection with the small size (2—3 μ) highly impedes an objective estimate of their actual length and of the position of the constrictions. At first I had the same impression as GUSTAFSSON, HEITZ, etc., that the chromo-

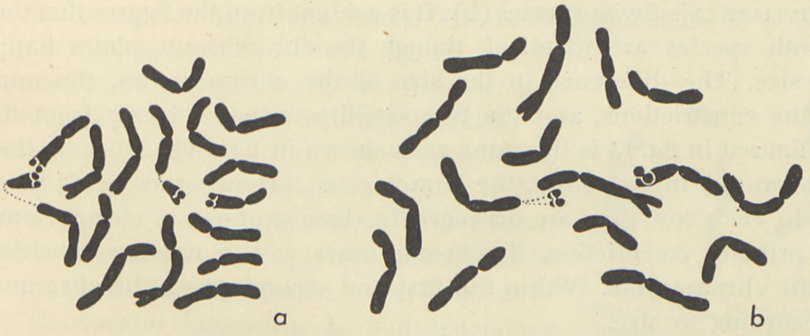

Fig. 13. Root tip mitoses. a: *T. obtusilobum* 2 n = 16. b: Sexual *Vulgaria* form from Switzerland 2 n = 16 (both figs. × 5200).

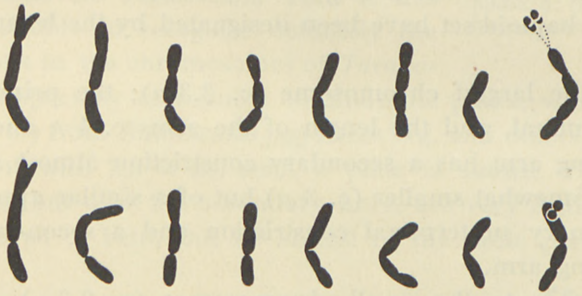

Fig. 14. Same mitosis as shown in fig. 13b, arranged in two rows, the homologous chromosomes being placed opposite each other (× 5200).

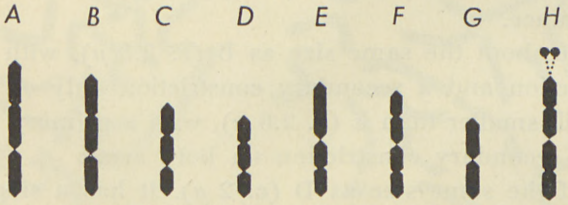

Fig. 15. The idiogram of the *Vulgaria* group. Lettering at the top of the figure (× 5200).

somes 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 individual chromosomes and their different modes of behaviour that a reliable idiogram could be drawn.

Diploids. — Fig. 13 shows mitoses of GUSTAFSSON's T. *obtusilobum* from Sweden (a) and CHRISTIANSEN's Swiss species (b). It is evident from the figures that the chromosomes in both species are identical, though the chromosome plates happen to be of different size. The difference in the size of the chromosomes, the number and position of the constrictions, and the two satellites appear clearly from the figures. The mitosis figured in fig. 14 is the same as is shown in fig. 13 b, but here the chromosomes are arranged in two rows, the homologous chromosomes being placed above each other. In each row they are arranged in three groups: 1) chromosomes with a submedian primary constriction, 2) chromosomes with a median constriction, and 3) the satellite chromosome. Within the first and second group the chromosomes are arranged according to size.

The idiogram which resulted from a study of numerous metaphases is represented in Fig. 15, the chrosomes arranged in the same way as in fig. 14. The eight chromosomes of the haploid set have been designated by the letters A—H as follows:

Chromosome A is the largest chromosome (c. 3.3 μ); the primary constriction is subterminal, and the length of the arms c. 1 μ and 2 μ respectively; the long arm has a secondary constriction almost at the middle.
— B is somewhat smaller (c. 3 μ) but of a similar appearance to A, with a primary subterminal constriction and a secondary constriction on the long arm.
— C belongs to the small chromosomes (c. 2.3 μ). It has a primary subterminal constriction and a secondary constriction on the long arm.
— D is a little smaller than C (c. 2 μ) but otherwise of entirely the same appearance.
— E is of about the same size as B (c. 2.8 μ), with a primary median constriction and a secondary constriction only on one arm.
— F is still smaller than E (c. 2.6 μ), with a primary median constriction and a secondary constriction on both arms.
— G is of the same size as D (c. 2 μ). It has a single medially placed primary constriction.
— H is of the same size as B and E (c. 3 μ), with a primary median constriction and a secondary constriction on each arm. At one end it is provided with a peculiar satellite attached by a long filament (fig. 16 d); the satellite is bent in such a way that it projects vertically from the metaphase plane. It is split like the chromosome and in cases in which the thread is not visible it may be very similar to the split terminal portion of the latter and consequently be difficult to recognise.

When, however, the satellites are seen in lateral view (fig. 16 c), as more rarely happens, they prove to be fairly long (up to c. 2 μ); their existence should probably be regarded as the main cause of earlier authors' records of doubtful chromosome numbers, which have later proved to be too high. Most probably they have regarded the satellites as independent chromosomes. The most frequent mode of occurrence of this satellite is seen in fig. 16 a and b.

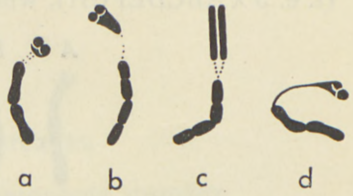

Fig. 16. The H chromosome from different cells. a and b: the most frequent forms, c: the satellite extended in the plane of the metaphase, d: the connecting thread in its entire length (all figures × 5200).

On account of the small size of the chromosomes it is, as stated above, attended with some difficulty to distinguish some of the chromosomes from each other, thus C and D, E and F, and sometimes F and G. The secondary constrictions may likewise be indistinct, a fact which is also known in other plants. Thus Flovik (1936) was unable to decide whether or not the chromosomes of *Ranunculus lapponicus* L. had secondary constrictions, though here the chromosomes are two or three times larger than in *Taraxacum*. That it has nevertheless been possible to recognise definitely the secondary constrictions in the chromosomes of *Taraxacum* is chiefly due to specially favourable chromosome plates, which resemble those figured by Flovik (l. c.) from *Ranunculus pygmaeus* Wg. and others. In fig. 20 e, from a hypoploid aberrant with 2 n = 23, such a plate is shown. Here especially the primary constrictions, but also the secondary ones, are very distinct, and the chromosomes are not curved or bent, but lie almost in the same plane.

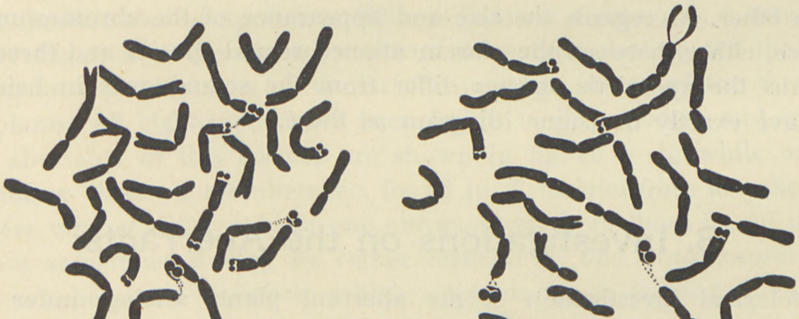

Fig. 17. Root tip mitoses. a: *T. polyodon*, normal plant 2 n = 24, b: *T. laciniosifrons*, normal plant 2 n = 24 (both figures × 5200).

Triploids. — My investigations of the apomictic *Vulgaria* species *T. polyodon* Dt. and *T. laciniosifrons* Wiinst. show that the 24 chromosomes of these species consist of 3 morphologically identic sets of chromosomes which correspond entirely to those of the diploid sexual *Vulgaria* species.

Fig. 17 shows mitoses of *T. polyodon* (a) and *T. laciniosifrons* (b). In the figures large and small chromosomes, the different position of the constrictions on the individual chromosomes, and the three satellite chromosomes in each plate are seen. The chromosomes in fig. 18 are the same as represented in fig. 17 a but here the chromosomes are arranged in rows according to the same principle as the chromosomes of the sexual species shown in fig. 14; very careful studies have convinced me that the only difference is that here we have 3 identical sets of chromosomes (i. e. 3 × ABCDEFGH), while the first had only two; in the figure the 3 sets are placed above each other. As regards the size and appearance of the chromosomes there is no difference, either, between the aforementioned sexual species and these apomictic species. Thus the apomictic species differ from the sexual ones in being triploid, but they have exactly the same idiogram as these.

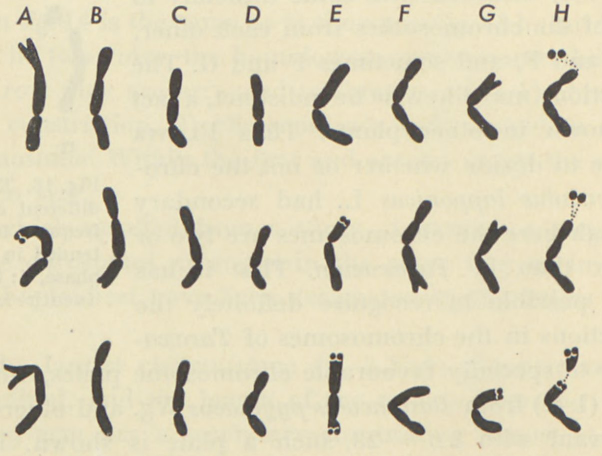

Fig. 18. Same mitosis as shown in fig. 17 a, arranged in three rows so that the homologous chromosomes are placed opposite each other (× 5200).

3. Investigations on the Aberrants.

A cytological investigation of the aberrant plants arising under cultivation showed that in most cases these plants had deviating chromosome numbers. Most frequently a reduction of the chromosome number had taken place, but sometimes the chromosome number was found to be increased; aberrant plants with unaltered chromosome numbers also occur, but are rather rare. Chromosome numbers differing from the euploid 8-series have not previously been demonstrated with certainty. It is true that Gustafsson (1932), by indicating chromosome numbers as 2 n = 23—24, 2 n = 24—25, etc., has previously suggested the possibility of the occurrence of numbers differing from the normal. However, from this we cannot conclude that he was dealing with chromosome aberrants. Most probably these statements are only indications of an uncertainty in the determinations owing to unsatisfactory material.

In the aberrant plants which have arisen from normal plants under cultivation the numbers 2 n = 23, 2 n = 24, 2 n = 25, 2 n = 26, 2 n = 38, and 2 n = 48 have been ascertained. As stated in part I of the present paper, the 2 n = 24 aberrant plants are of rather rare occurrence. The aberrant types which have arisen regularly and repeatedly are, in addition to *gigas*, such as have 2 n = 23. These types have been subjected to a close investigation in order, if possible, to ascertain their exact chromosome constitution.

A. Aneuploid Chromosome Aberrants.

1. Aneuploid aberrants with a reduced chromosome number.

The aberrants which have arisen directly from normal plants are here called primary aberrants; secondary aberrants have arisen from primary aberrants, and tertiary from secondary.

a. Primary aberrants.

As mentioned more fully in part I, eight different 2 n = 23 aberrant types were ascertained in *T. polyodon*, called *aberr. elegans, truncata, hamosa, plumosa, pygmaea, tenuis, crassifolia*, and *olivacea*. An entirely analogous series was found in *T. laciniosifrons*, only the last-mentioned aberrant, *olivacea*, has not yet been found here.

The chromosome equipment is different in these eight types. A detailed morphological investigation of the chromosomes of these types has shown that each of the eight aberrant types lacks its particular chromosome in one of the three sets of the normal plants. All eight types have been found in *T. polyodon*, and mitoses of the primary aberrants of this species are shown in fig. 19 a—h, while mitoses of the seven primary chromosome aberrants found in *T. laciniosifrons* are shown in fig. 20 a—g. These mitoses differ only in one chromosome from those found in the normal plants, but sometimes it may be rather difficult to find chromosome plates from which it can be stated definitely which chromosome is lacking. It is due, among other things, to the fact that in some of the primary aberrants the roots are much more difficult to fix and stain properly than in the normal plants.

In fig. 21 is shown schematically which chromosome is lacking in each of the eight aberrant types. In the top line the designation of the chromosome is found, in the first column the name of the aberrant in question. Only the seven chromosomes of the deficient set are figured, the two normal sets of 8 having been omitted; thus it appears directly from the figure which chromosome is lacking in each aberrant. Analogous aberrants in different species lack analogous chromosomes.

Fig. 19. *T. polyodon.* Root tip mitoses of the eight primary aberrants with $2n = 23$. a: *olivacea;* b: *truncata;* c: *hamosa;* d: *elegans;* e: *crassifolia:* f: *pygmaea;* g: *plumosa:* h: *tenuis* (all figs. × 5200).

The chromosome equipment of the eight aberrants may be expressed as follows:

aberr. olivacea .... $2n = 8 + 8 + (8 - A)$, see fig. 19 a
aberr. truncata .... $2n = 8 + 8 + (8 - B)$, see figs. 19 b, 20 a
aberr. hamosa .... $2n = 8 + 8 + (8 - C)$, see figs. 19 c, 20 b
aberr. elegans .... $2n = 8 + 8 + (8 - D)$, see figs. 19 d, 20 c
aberr. crassifolia .... $2n = 8 + 8 + (8 - E)$, see figs. 19 e, 20 d
aberr. pygmaea .... $2n = 8 + 8 + (8 - F)$, see figs. 19 f, 20 e
aberr. plumosa .... $2n = 8 + 8 + (8 - G)$, see figs. 19 g, 20 f
aberr. tenuis .... $2n = 8 + 8 + (8 - H)$, see figs. 19 h, 20 g

Fig. 20. *T. laciniosifrons.* Root tip mitoses of the seven primary aberrants with 2 n = 23. a: *truncata;* b: *hamosa;* c: *elegans:* d: *crassifolia;* e: *pygmaea:* f: *plumosa;* g: *tenuis* (all figs. × 5200).

That precisely eight different 2 n = 23 aberrants and not more were found strongly suggests that the three chromosome sets of the normal plants are alike not only morphologically, but on the whole also genetically. In the opposite case there would be the probability of more than these eight chromosome aberrants being produced.

b. Secondary aberrants.

The progeny of the primary aberrants are largely identical with the mother plant; however, a number of secondary aberrant plants are found among them.

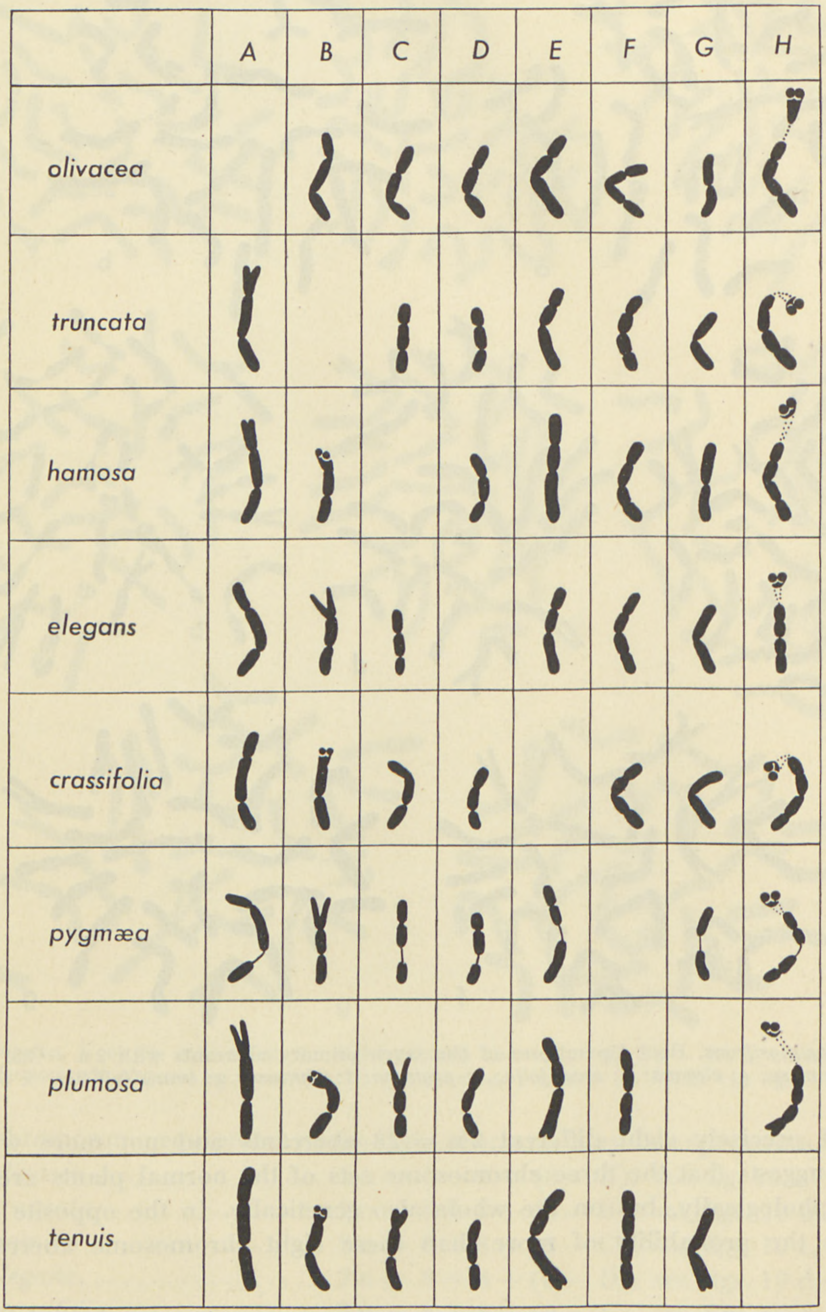

Fig. 21. Table showing which chromosome in the idiogram is lacking in the various primary 2 n = 23 aberrants (× 5200).

A few of these have still 2 n = 23, but in others a fresh chromosome aberration has taken place, and these have only 2 n = 22. The morphological characteristics of these plants have their counterpart in their chromosome constitution. Every secondary aberrant combines the characters of two different primary aberrant types, and similarly the cytological investigation shows that it lacks precisely those two chromosomes the loss of each of which gives rise to each of the aberrant plant characters in question. The reliability of the cytological analysis is evident e. g. from the fact that the secondary aberrant *pygmaea* → *tenuis* in *T. polyodon* was found to lack the F- and H-chromosomes before the primary *tenuis* type had been ascertained in this species (fig. 22 d).

The two chromosomes lacking in the secondary aberrants are always different ones, the contemporary loss of two homologous chromosomes having not hitherto been ascertained. Probably such combinations as 24 — 2 A or 24 — 2 B, etc., are lethal.

It has been mentioned above that primary aberrants with an increased chromosome number arise now and then. Similarly, secondary aberrants have been found in which an increase in the chromosome number has taken place. Thus a very peculiar aberrant of *T. laciniosifrons aberr. elegans* had the chromosome number 2 n = 29. Similarly, secondary aberrants may in this way again attain 2 n = 24.

c. Tertiary aberrants.

Hypoploid aberrants of the third order, which morphologically combine the characters of three different aberrant types, have as a rule the chromosome number 2 n = 21 (fig. 22 c). They arise through the loss of one more chromosome. Exceptionally, however, there may be a loss of several chromosomes at the same time. Thus 2 n = 19 was found in a tertiary aberrant (fig. 22 a), the mother plant of which was *T. laciniosifrons aberr. elegans* → *hamosa* and had 2 n = 22 (i. e. 2 n = 24 less D less C). But in this tertiary aberrant, to which rather *plumosa* characters had been added, the E and the F chromosome, besides the D, C, and G chromosomes, were lacking. On account of the weakness of the plant (it did not flower) it was difficult to decide from its morphological appearance which types it represents. Another tertiary aberrant, likewise derived from a *T. laciniosifrons aberr. elegans* → *hamosa,* proved to have 2 n = 20 (fig. 22 b). A closer analysis of its chromosomes was not made.

2. Aneuploid aberrants with an increased chromosome number.

As mentioned above, some other aneuploid chromosome numbers were ascertained in aberrants derived from normal triploid plants; thus the chromosome numbers 2 n = 25, 2 n = 26, and 2 n = 38 were found. So far no analysis of their chromosome equipment has been made.

Fig. 22. Root tip mitoses. a: *T. laciniosifrons.* Offspring with 2 n = 19 of a secondary *elegans* → *hamosa* aberrant; b: *T. laciniosifrons.* Derivative plant with 2 n = 20 of a secondary *elegans* → *hamosa* aberrant; c: *T. polyodon.* A tertiary *pygmaea* → *olivacea* → *tenuis* aberrant with 2 n = 21; d: *T. polyodon.* A secondary *pygmaea* → *tenuis* aberrant with 2 n = 22; e: *T. polyodon. Gigas* with 2 n = 44 from a chimaeric secondary *pygmaea* → *tenuis* aberrant; f: *T. polyodon. Gigas* with 2 n = 46 of a primary *pygmaea* aberrant (all figs. × 5200).

B. Aberrant Plants with an Unaltered Chromosome Number.

Of the aberrants derived from normal plants some have been found to have the unaltered chromosome number, 2 n = 24. A close investigation of the chromosome morphology of these 2 n = 24 plants has not yet been completed. Such plants are rather rare and arise quite casually, unlike the 2 n = 23 aberrants and the *gigas*, which arise fairly often and regularly in various species. In the 2 n = 24 aberrant plants it may be a case of deficiencies, involving only small parts of one or more chromosomes, or possibly other phenomena.

C. Polyploid Aberrants.

An aberration of frequent occurrence is a doubling of the chromosome number, in which way hexaploid plants with 2 n = 48 arise from the triploids. Thus the *gigas* plants have six morphologically identic chromosome sets in the somatic cells. A mitosis from *T. laciniosifrons aberr. gigas* is shown in fig. 23. It will be seen that the chromosomes are rather short and distinct, so it is fairly easy to count them with certainty. On the other hand the individual characteristics of the chromosomes are less marked than in the other mitoses figured; cf. fig. 22 e and f, which are likewise derived from *gigas* plants.

Just like the normal plants, primary chromosome aberrants may produce *gigas*, i. e. secondary aberrants with 2 n = 46 (fig. 22 f). The secondary 2 n = 22 aberrants may likewise develop a *gigas* with 2 n = 44 (fig. 22 e), but these plants are usually weak.

The primary *gigas* as well as the other *gigas* forms may in their turn produce aberrants by losing one or more chromosomes. Thus a primary *gigas* of *T. polyodon* segregated a plant with 2 n = 47, another with 2 n = 45. These different *gigas* plants have not been investigated cytologically to any great extent.

Fig. 23. *T. laciniosifrons* aberr. *gigas*, 2 n = 48 (× 5200).

4. Discussion.

Chromosome aberrants are known from many instances within the vegetable kingdom. Most commonly the aberrant plants have one chromosome too much, they are so-called trisomics; this is natural in so far as the equilibrium of the genom is less disturbed by the addition of an extra chromosome than by the loss of a chromosome. In the great majority of cases in which 2 n less 1 aberrants occur, the normal chromosome equipment is of a polyploid nature, so that we can hardly speak of monosomics. This is also the case in *Taraxacum*, where the plants are triploid.

Apomictic plants have the advantage over the sexual species that mutations, aberrations, and other genotypical alterations are transmitted to the whole progeny, so that it is at once possible to preserve any mutation in so far as the particular plant is capable of surviving and is not quite sterile, while mutations are often difficult to preserve in the sexual species.

Aneuploid series are known from a number of plants. The best known example is BLAKESLEE-BELLING-FARNHAM's *Datura* series (1920), where, however, we are concerned with $2n + 1$ aberrants. Entirely parallel to *Taraxacum* are the $2n - 1$ series of *Nicotiana* (CLAUSEN 1932, OLMO 1935). However, the earlier known cases always belong to sexual species, in which the "monosomic" constitution mostly arises by non-disjunction at meiosis. The aberrant sexual cells are capable of functioning either by selfing (CLAUSEN & GOODSPEED 1926 a, RUTTLE 1927, AVERY 1929 in *Nicotiana*, GRIESINGER 1939 in *Hyoscyamus niger*) or by back-crossing of species hybrids to one of the parent species (CLAUSEN and GOODSPEED 1926 b, LAMMERTS 1932, OLMO 1935 in *Nicotiana*). Several *Nicotiana* species, i. a. *N. tabacum*, are thought to be of a polyploid nature (GOODSPEED & CLAUSEN 1928).

Another way in which $2n - 1$ aberrants have been found to arise is by abnormal mitoses. They will then often appear as chimaeras (Mc CLINTOCK 1929 in *Zea*, BLAKESLEE & BELLING 1924 in *Datura*).

The *Taraxacum* series differs from the cases previously observed by having arisen in an obligate apomict. The chromosomal aberration in *Taraxacum* is probably due in part to abnormal mitoses, but it may possibly also be brought about during the formation of the embryo sac even though a typical meiosis is lacking.

An abnormal mitosis may take place in any somatic cell. Thus a few cells in the root tips have often a chromosome more or less than the normal ones. A doubling of the chromosomes may likewise occasionally occur in somatic cells; fig. 22 e shows a mitosis in a root cell in which the chromosome number had been doubled and which had $2n = 44$, while the other parts of the plant had $2n = 22$, i. e., a secondary chromosome aberrant. If a chromosome aberration takes place in one of the meristematic cells, the shoot in whole or in part (either as a sectorial or a periclinal chimaera) will be affected by the aberration.

So far hypoploid aberrants have not been found to have arisen by abnormal mitoses in *Taraxacum*, since chimaeras have not yet been seen. The aberrants have always turned up in seed-progenies.

As already mentioned in part I of the present paper, however, a number of cases of chimaeric aberrant plants have been ascertained, but these plants have always an increased or an unaltered chromosome number, thus $2n = 24$, $2n = 25$, or $2n = 26$. The aberrant *gigas* likewise occurs very frequently as a chimaera. Here then, the aberrations seem to some extent to be due to abnormal mitoses.

We shall, however, refrain from a further discussion in this place of the origin of the aberrations. This question will be dealt with more fully in a future paper in connection with the results of investigations, not yet completed, of the cytology of the formation of the sexual cells, which alone can provide the necessary concrete basis for such a discussion.

There may, however, be some reason even now to utilise the cytological results for a discussion of the nature of the triploid species of *Taraxacum*, that is to say, the way in which they may have arisen. It must be assumed that diploid species of *Taraxacum* with 2 n = 16 are the original species, no matter whether they were sexual or apomictic, and from them the triploid and other polyploid forms then must have been derived. The question is now whether we are concerned with autotriploids or allotriploids, that is to say, whether all the three chromosome sets are identic (homologous) or whether they are different. If the three sets are different, it might possibly be demonstrated by a morphological examination of the chromosomes.

The theory has been propounded by ERNST (1917, 1918), ROSENBERG (1917), and WINGE (1917) that hybridisation is the cause of apomixis. The majority of the apomictic species are triploid, and they might then possibly have arisen by hybridisation between a diploid and a tetraploid sexual species. It is true that it has not yet been possible to produce an apomictic triploid species by hybridisation of parent species, both purely sexual, so the fundamental change from amphimixis to apomixis seems to be very complicated. In this connection it is also of interest to note that the known tetraploid and hexaploid species of *Taraxacum* are likewise apomictic.

GUSTAFSSON (1932) has discussed the possibility of concluding from the cytological behaviour whether the 2 n = 24 forms of *Taraxacum* can be regarded as auto- or allotriploids. On the basis i. a. of the characteristics of the somatic chromosome equipment GUSTAFSSON (1932) arrives at the result that allotriploidy is absolutely the most probable. He says about this subject (l. c., p. 59): "Bis jetzt untersuchte, deutliche Fälle gibt es nur wenige, aber sämtliche berechtigen zu der Annahme, dass Allopolyploidie die Ursache der Chromosomenvermehrung ist. So z. B. besitzt 1929: 11 (Fig. 48) unzweideutig zwei ansehnliche Chromosomen und bei 1930: 416 (Fig. 27 u. 52) wurde in mehreren Kernplatten ein Chromosom wahrgenommen, das bedeutend länger als die übrigen war. Gleichzeitig war das Verhältnis bei 1930: 221 und 223 (Fig. 50 u. 51)." Three of these plants belong to species of the *Vulgaria* group.

On the other hand BERGMAN (1935) investigated a triploid apomictic *Hieracium umbellatum*. On the basis of the chromosomatic morphology and the number of the associations during the meiosis the author concludes that the plant is autotriploid.

The results arrived at by us, i. e. the morphologically identic three sets of 8 chromosomes in the triploid *Taraxaca*, and especially the fact that only eight different primary chromosome aberrants have been found, are in favour of the view, that these species are autotriploid.

It should be mentioned here that primary aberrants of the same type may sometimes exhibit minor differences of such a subtile nature that they can only be observed when progenies of the plants are cultivated in rows side by side in the experimental field. As stated in part I, similar differences may be observed between different strains within the species. However, this can be no essential objection against the assumption of autotriploidy, since these small differences may be due to point mutations, or possibly small deficiencies, a question which will not be treated here.

Morphological investigations of the chromosomes in various other species of *Taraxacum*, including those with 2 n = 32, 2 n = 40, and 2 n = 48, have likewise been made; the results of these studies will be published later. More detailed studies of the morphology of the chromosomes may possibly serve to throw some light on the interrelationship of the different groups within the genus.

On the completion of the present paper the authors wish to express their thanks to the colleagues and institutions who have supported us in various ways during the investigation.

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III. SUMMARY

The present investigation deals with spontaneous aberrants in apomictic *Taraxaca* of the *Vulgaria* group ($2n = 24$).

1. Various microspecies produce to a great extent analogous aberrants, which form well delimited types. The aberrants accordingly constitute parallel series which transgress the specific limits.

2. The aberrants which are analogous for a number of microspecies comprise two categories, 1) aneuploid chromosome aberrants ($2n = 23$), of which eight morphologically well separated types were found, which were denoted *aberr. elegans, aberr. truncata, aberr. plumosa, aberr. hamosa, aberr. pygmaea, aberr. tenuis, aberr. olivacea,* and *aberr. crassifolia* (cf. Pls. I, II, and VI, text-figs. 2, 3, 4, and 5); and 2) polyploid aberrants (*aberr. gigas* $2n = 48$) (cf. Pls. III and IV, text-figs. 10, 11, and 12).

3. The primary $2n = 23$ aberrants produce secondary aberrants with the chromosome number $2n = 22$. These form parallel series to the primary aberrants, each of them combining the characters of the mother plant and one of the other primary aberrants. Example: secondary *aberr. plumosa* → *elegans,* i. e. the *elegans* aberrant of *aberr. plumosa* (cf. Pl. IV).

4. Similarly, the secondary aberrants are able to produce tertiary aberrants with the chromosome number $2n = 21$. Example: tertiary *aberr. elegans* → *hamosa* → *plumosa.*

5. A rapid decrease in vitality and power of reproduction is generally found in the successive steps of aberration.

6. Just as the original species, the aberrants are able to produce polyploids by a doubling of their chromosome number. These polyploids show, as a rule, a marked decrease in vitality.

7. As regards the frequency with which the aberrants arise the following facts may be given: a) The various microspecies show an unequal tendency to produce aberrants. The two microspecies most thoroughly studied, *T. laciniosifrons* Wiinst. and *T. polyodon* Dt., behaved similarly and yielded c. 0.7 $^0/_0$ $2n = 23$ aberrants and c. 0.8 $^0/_0$ *gigas* aberrants, but in other species a higher or lower frequency of aberration was ascertained. b) The individual aberrant types are formed with different frequency. c) The frequency of aberration in the $2n = 23$ aberrants is generally higher than in the respective main species, but differs much in the different aberrant types. The highest occurs in *aberr. elegans* with a frequency of about ten times that of the main species in regard to production of chromosome aberrants (secondary aberrants, $2n = 22$). *Aberr. pygmaea* is especially liable to produce polyploids. It produces *gigas* aberrants about four times as frequently as the respective main species.

8. *Gigas* aberrants frequently arise as chimaeras, for which reason it is assumed that the polyploid constitution is initiated by an abnormal mitosis in the vegetative tissues.

9. Chimaeric plants whose aberrant sector is not of a *gigas* character have likewise been ascertained. The aberrant part of such plants had in certain cases an unaltered chromosome number ($2n = 24$), in other cases an increased chromosome number ($2n = 25$, $2n = 26$).

10. Aneuploid aberrants with loss of chromosomes ($2n = 23$) have not hitherto been met with as chimaeras and are therefore assumed to have arisen by irregularities during the initiated, but not completed, meiosis.

11. By a cytological investigation of two diploid sexual species ($2n = 16$) and several apomictic species ($2n = 24$) it was possible to establish the idiogram of the *Vulgaria* group (fig. 15); the basic set consists of eight chromosomes which differ morphologically in size, constrictions, and satellites. The somatic number in the sexual species is 2×8 (fig. 14), in the apomictic species 3×8 (fig. 18).

12. The chromosome lacking in each of the eight primary aberrant types could be shown to be a different one in each case (fig. 21). The chromosome complement of these aberrants can thus be written $8 + 8 + (8 - A)$, $8 + 8 + (8 - B)$, etc., the eight chromosomes in the idiogram being named A, B, C, D, etc.

13. The secondary $2n = 22$ aberrants lack two chromosomes in one of the haploid sets. Thus, for instance, *aberr. elegans* → *hamosa* lacks the two chromosomes each of which produces *aberr. elegans* and *aberr. hamosa* respectively.

14. Tertiary $2n = 21$ aberrants similarly lack three chromosomes.

15. The chromosome numbers $2n = 20$ and $2n = 19$ have exceptionally been found in aberrant plants derived from secondary $2n = 22$ aberrants.

16. Chromosome aberrants of the type $8 + (8 - A) + (8 - A)$, or $8 + (8 - B) + (8 - B)$, etc., have never been met with, such plants being probably not viable.

17. The fact that eight and not more primary aberrants of the type $2n = 23$ have been found affords strong evidence for the hypothesis that the apomictic triploid *Taraxaca* are of an autotriploid nature. Consistent with this view is the fact that the somatic chromosome complement of these plants consists of three morphologically identical sets of eight chromosomes each.

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Taraxacum laciniosifrons Wiinst. and *Taraxacum polyodon* Dt. with 2 n = 23 aberrants. a—e: *T. laciniosifrons*; f—j: *T. polyodon*; a, f: normal plants; b, g: *Aberr. elegans*; c, h: *Aberr. truncata*; d, i: *Aberr. plumosa*; e, j: *Aberr. hamosa*. ($^1/_4$ natural size).

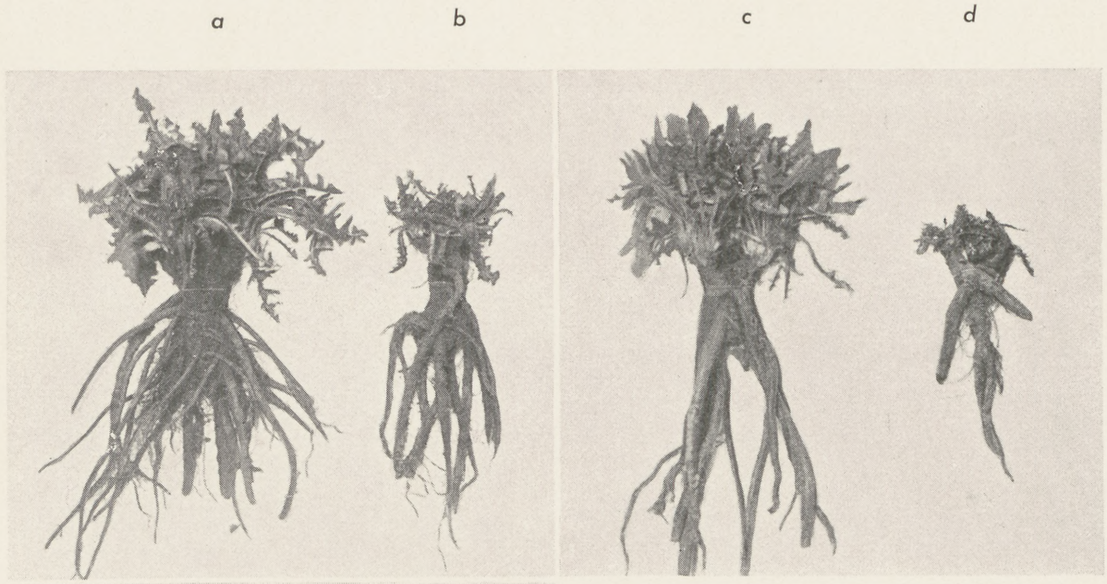
PLATE II

Taraxacum laciniosifrons Wiinst. and *Taraxacum polyodon* Dt. with $2n = 23$ aberrants. a—e: *T. laciniosifrons*; f—j: *T. polyodon*; a, f: normal plants; b, g: *Aberr. pygmaea*; c, h: *Aberr. tenuis*; i: *Aberr. olivacea*; e, j: *Aberr. crassifolia*. ($^{1}/_{4}$ natural size).

PLATE III

Taraxacum laciniosifrons Wiinst. and *Taraxacum polyodon* Dt. with *gigas* aberrants (2 n = 48). a—b: *T. laciniosifrons*; c—d: *T. polyodon*; a, c: normal plants; b, d: *Aberr. gigas*. ($^1/_4$ natural size).

PLATE V



Normal and *gigas* plants three years old, April. a, b: *T. laciniosifrons* Wiinst; c, d: *T. polyodon* Dt; e, f: *T. bracteatum* Dt; a, c, e: normal plants; b, d, f: *gigas* plants. (about $^1/_5$ natural size)

PLATE VI

Achenes of *Taraxacum laciniosifrons* Wiinst. and *Taraxacum polyodon* Dt. and of their $2n = 48$ and $2n = 23$ aberrants. a—j and A—J: *T. laciniosifrons*; k—t and K—T: *T. polyodon*; a, A and k, K: *Aberr. gigas*; b, B and l, L: normal plants; c, C and m, M: *Aberr. elegans*; d, D and n, N: *Aberr. truncata*; e, E and o, O: *Aberr. plumosa*; f, F and p, P: *Aberr. hamosa*; g, G and q, Q: *Aberr. pygmaea*; h, H and r, R: *Aberr. tenuis*; s, S: *Aberr. olivacea*; j, J and t, T: *Aberr. crassifolia*. (a—t: $^2/_1$; A—T: $^4/_1$)