CYTOTAXONOMIC STUDIES ON RUMEX SUBGENUS LAPATHUM SECTION AXILLARES

by

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Abstract.

The Axillares section of Rumex subgenus Lapathum has been studied from the cytological and taxonomic point of view and is found to contain a polyploid series. In the subsection Salicifolii, Rumex altissimus, R. utahensis, R. crassus, R. pallidus, R. transitorius, R. sibiricus and R. mexicanus subsp. triangulivalvis have 2n = 20. R. venosus representing the subsection Venosi has 2n = 40, and R. verticillatus from the subsection Verticillati has 2n = 60. Meiosis studied in some species of the Salicifolii is generally normal with the exception of the presence of tripartite bivalents in several of the species which are thought to be analogous to T- chromosomes in inbred rye. Plants of R. pallidus, from seeds obtained from Göteborg, Sweden, showed irregularities in meiosis indicating a hybrid origin. R. triangulivalvis has been reclassified as R. mexicanus subsp. triangulivalvis.

I. INTRODUCTION.

The genus Rumex, although relatively unimportant from the economic standpoint, has been a great aid in research, as was aptly pointed out by Löve (1943), serving in "an attack on the cytogenetics, taxonomy and speciation of plants in order to prepare the ground for a joint analysis of the evolutionary processes". It consists of approximately 250 species, members of which are world wide in distribution. The genus in its entirety had been monographed by early workers (Campdera, 1819; Meisner apud De Candolle, 1856). In 1893, Trelease listed twenty-one species in his "Revision of the species of Rumex occuring north of Mexico." Since Trelease's paper fourteen species and some varieties have been reported. A thorough revision of the North American species of Rumex was undertaken by Rechinger (1937) who listed forty-nine species and four hybrids, and attempted a natural arrangement of these species.

In recent classifications the species of Rumex have been divided into three subgenera with well defined morphological and cytological characteristics. These are: Acetosella (Meisn.) Rech. fil., Acetosa (Campd.) Rech. fil., and Lapathum (Campd.) Rech. fil. Of these, the subgenus Acetosella is the smallest with only four dioecious perennial species. The basic number of this group has been reported as x = 7 by Löve (1943). The second subgenus, Acetosa, comprises about a hundred species which have been grouped in four sections with different basic numbers by Löve (1943, 1944). These are: Acetosa (=Euacetosae Löve),(x = 7,8),

Hastati Löve, (x = 9), Scutati Löve, (x = 10), and Vesicarii Löve,(x = 9).

The largest subgenus Lapathum, comprising some hundred and fifty species, has been divided into three sections mainly on morphological grounds. These are: Simplices Rech. fil., Axillares Rech. fil., and Platypodium Willd. The section Simplices comprises erect plants without axillary shoots, while the section Axillares consists of plants with numerous axillary shoots. The remaining section Platypodium is monotypic with R. bucephalophorus its sole species, which has a low spreading growth habit. According to Löve (1943), the first mentioned section is characterized by the basic number x = 10, the two others having the basic number x = 8 in the material so far investigated.

In contrast to the rather extensive cytological work done in the subgenera Acetosella and Acetosa, very little is known cytologically in the subgenus Lapathum and almost nothing in its section Axillares.It is this section which is considered cytologically and taxonomically in the present investigation.

The section Axillares has been divided by Rechinger (1937) into three subsections: Venosi Rech. fil., Verticillati Rech. fil., and Salicifolii Rech. fil. Venosi consists of one species Rumex venosus Pursh; Verticillati is made up of three species, R. fascicularis Small, R. floridanus Meisn. and R. verticillatus L.; and the remaining species fall into the subsection Salicifolii. There are fourteen species listed by Rechinger in the latter subsection which, though distinguishable on the whole

by easily visible characters, are sufficiently close to each other in gross morphology to make Salicifolii an apparently natural group. This is also supported by the present investigation of this group on the cytological level. The members of this subsection are: R. spiralis Small, R. altissimus Wood, R. ellipticus Greene, R. mexicanus Meisn., R. Berlandieri Meisn., R. triangulivalvis (Danser) Rech. fil., R. lacustris Greene, R. transitorius Rech. fil., R. pallidus Bigel., R. sibiricus Hulten, R. utahensis Rech. fil., R. crassus Rech. fil., R. salicifolius Weinm., and R. californicus Rech. fil.

In the present investigation nine species are taken into consideration. The subsections Venosi and Verticillati are represented by R. venosus and R. verticillatus respectively, while the remaining seven species fall into the subsection Salicifolii. These are: R. altissimus, R. utahensis, R. crassus, R. pallidus, R. transitorius, R. sibiricus and R. triangulivalvis.

II. MATERIALS AND METHODS.

1. Material.

The materials used in the present study were obtained, through the courtesy of Dr. A. Löve, as seed samples from the different sources listed below. It must be mentioned in this connection that the identity of the majority of the samples had to be determined by comparing the plants grown from the seeds with valid descriptions or herbarium sheets, since the specific names under which they were received were found to be incorrect.

R. venosus

1) Division of Botany and Plant Pathology, Ottawa. Collected by L. Jenkins, 1951, No. 875, with the locality given as Kindersly, Saskatchewan.
2) National Herbarium of Canada, Sheet No. 16942. Collected by A.E. Porsild, 1948. Locality Lethbridge, Alberta.

R. verticillatus

Division of Botany and Plant Pathology:

1) Locality St. Jean Co., St. Jean, Quebec. Collected by Lionel Cinq-Mars, 1952.
2) Locality Brittania, Ontario. Collected by C. Frankton, 1953, N. 1445.
3) Locality Shirley Bay, Carlton Co., Ont. Collected by W.G. Dore and D. Erskine, 1952, No 14091.

R. altissimus

1) Munich, Germany- listed as R. salicifolius Weinm.

2) Botanical Garden, Basel, Switzerland,-listed as R. salicifolius Weinm.

R. utahensis

National Herbarium of Canada, Sheet No. 113824. Collected by H. J. Scoggan, 1948. No. 4963. Locality Grand Rapids, Manitoba- listed as R. altissimus.

R. crassus

Division of Botany and Plant Pathology. Collected by J.K. Brenckle, 1951, No. 51281. Locality Douglas Co., Oregon.

R. transitorius

University of British Columbia and Botanical Garden- listed as R. mexicanus.

R. pallidus

1) Montreal Botanical Garden, Montreal, Quebec.

2) Botanical Garden, Göteborg, Sweden- listed as R. triangulivalvis.

R. sibiricus

Dominion Arboretum, Ottawa, Canada. Locality Dawson, Yukon, Canada.

R. triangulivalvis

1) Botanical Garden, University of Oslo, Oslo, Norway.

2) Botanical Garden, Helsinki, Finland - listed as R. mexicanus Meisn.

3) Botanical Garden, Turku, Finland -listed as R. mexicanus Meisn.

4) Dominion Arboretum, Ottawa,Canada.

5) Botanical Garden, Lund, Sweden.- listed as R. salicifolius Weinm.

6) Botanical Institute, Rome, Italy- listed as R. salicifolius Weinm.

7) Division of Botany and Plant Pathology, Ottawa, Canada. Locality Bonneclare River, Ont. Collected by W.H. Minshall, 1945, No. 3547.

8) National Herbarium Of Canada:

a) Sheet No. 224926. Collected by H.J. Scoggan, 1953, No. 11565. Locality Morris, Manitoba.

b) Sheet No. 209486. Collected by H.J. Scoggan, 1953, No. 9874. Locality Brandon, Man.- listed as R. mexicanus Meisn.

2. Methods.

Most of the seeds were germinated and planted in the greenhouse in pots in the spring of 1954, and later transplanted to the field where they flowered the same year. The seeds which were available only in small quantity and those which were received too late for field planting were grown to maturity in the greenhouse; of these only a small proportion flowered. The plants grown in the field formed bisexual flowers, whereas those grown in the greenhouse produced only female flowers. Thus meiosis could not be studied in R. venosus, R. verticillatus, R. utahensis, R. crassus and R. sibiricus.

For the determination of the somatic chromosome numbers, root tips were collected from seeds germinated in petri-dishes as well as from potted plants. Various methods were tried for staining the chromosomes. It was found that the chromosomes showed no stain with Feulgen squash method or Tjio and Levan's (1951) oxyquinoline method. The best results were obtained either by the use of Navashin-Karpechenko's fluid or Lewitsky's fixative (8 parts of 1% chromic acid to 2 parts 10% formalin). Following fixation the usual schedule was followed to make paraffin blocks. Sections were cut at 10 micra. After being mordanted overnight in 1% chromic acid, the sections were stained according to the iodine-gentian-violet method (Newton and Darlington, 1929) with the modification of the use of an aqueous solution of iodine and potassium iodide instead of an alcoholic one.

For the study of meiosis, the flower buds were fixed in modified Carnoy's solution (absolute alcohol: chloroform: glacial acetic acid:: 6:3:1), and could be kept in the fixative for an indefinite period of time giving good results even after five months. The procedure followed for staining was:

1) Pollen mother cells dissected into iron-acetocarmine (Belling's) and squashed.
2) Slide separated from coverslip by immersion in 95% alcohol.
3) Slide and coverslip reassembled, the mount made permanent in euparal.

The observations were made under a 120x oil immersiom lens, and the drawings by aid of a camera lucida at table level.

III. MORPHOLOGY AND DISTRIBUTION.

According to Rechinger (1937) the three subsections of Axillares are well defined by clear morphological characters. The subsection Venosi is represented by R. venosus which has grainless, conspicuous valves, more than 20 mm. broad, in contrast to the much smaller (up to 12 mm. broad) valves of the other two subsections. The subsection Verticillati is characterized by pedicels that are 2.5 - 5 times longer than the fruit, while the members of the subsection Salicifolii have pedicels at most twice as long as the fruit. It is obvious that the difference between the last two subsections is only quantitative, based simply on the comparative length of the pedicels. In other morphological characters the members of the two groups are very close to each other and, as will be seen later, the quantitative difference seems to be due to degree of polyploidy.

A key to species studied here is given below to show the morphological differences between the subsections and their constituent members.

Key to the Rumex Species Studied (modified from Rechinger, 1937)

Flowers usually androgynous, leaves never hastately lobed...
... Subgenus Lapathum

Stems erect, ascending, or procumbent, with axillary shoots...
.... Section Axillares

Valves wider than 20 mm., grainless, with a fine, double reticulation, ocreae conspicuous..... R. venosus

Valves much smaller, ocreae smaller, appressed.

Pedicels 3 - 5 times longer than fruit, panicle open, leaves 5 - 6 times longer than broad.... R. verticillatus.

Pedicels at most twice as long as fruit.

Leaves ovate-lanceolate, broadest below the middle, valves more than 4,5 mm. long ..... R. altissimus.

Leaves usually narrower, lanceolate or linear-lanceolate.

Valves grainless, crenulate at base, fruiting panicle small, compact..... R. utahensis.

One or all valves grain-bearing.

Grains occupying nearly the whole breadth of the valve.

Valves with only one grain. Valves relatively large, 4 - 5 mm. long, leaves 2- 3 times long as broad...R.crassus.

Valves smaller, all with grains.

Valves 3 - 4 mm. long, grains very large, leaves 2 - 3 times long as broad.....R. transitorius.

Valves 3 - 4 mm. long, grains smaller, leaves narrower.....R. pallidus.

Valves 2.5 - 3 mm. long, longer than grain....R. sibiricus.

Grains much narrower than the breadth of the valves (margin of the valve at least as broad as the grain)

Valves about 4 mm. long, nutlets 2.5 mm. long... .... R. mexicanus.

Valves about 3 mm. long, nutlets about 2 mm. long... .... R. triangulivalvis.

Taxonomical and Distributional Considerations:

R. venosus-

Distribution: Basin of the Saskatchewan River, Canada, weastern United States from Washington and Nevada to the Missouri River Basin and Texas (Fig. 1).

R. verticillatus-

Distribution: Lower part of southeastern Canada and the eastern and middle United States (Fig. 1).

R. altissimus-

Distribution: Lower parts of the eastern and middle United States to Arizona (Fig. 2). Introduced to Europe.

There is considerable confusion as to the correct name of this species. Wood (1853) described R. altissimus as thick leaved, 3 - 5 inches long, 1/4 - 1 inch broad, sepals thin, entire and veiny, the inner broadest and always naked, the second bearing a large tubercle, and the third a small one or none. According to Trelease (1893), Meisner (1856) regarded R. altissimus the same as R. Claytonii Camp. However Campdera's (1819) description, "R. vaginis obsolete laceris, sepalis internis denum ovato-rotundatis obtusis integris vix granulatis", is inadequate for identification of the species without reference to his type specimen. Unfortunately neither Wood's nor Campdera's type specimen is available for observation. The plant identified as R. altissimus by taxonomists since Trelease's time has been so named according to the interpretation of Trelease (1893),

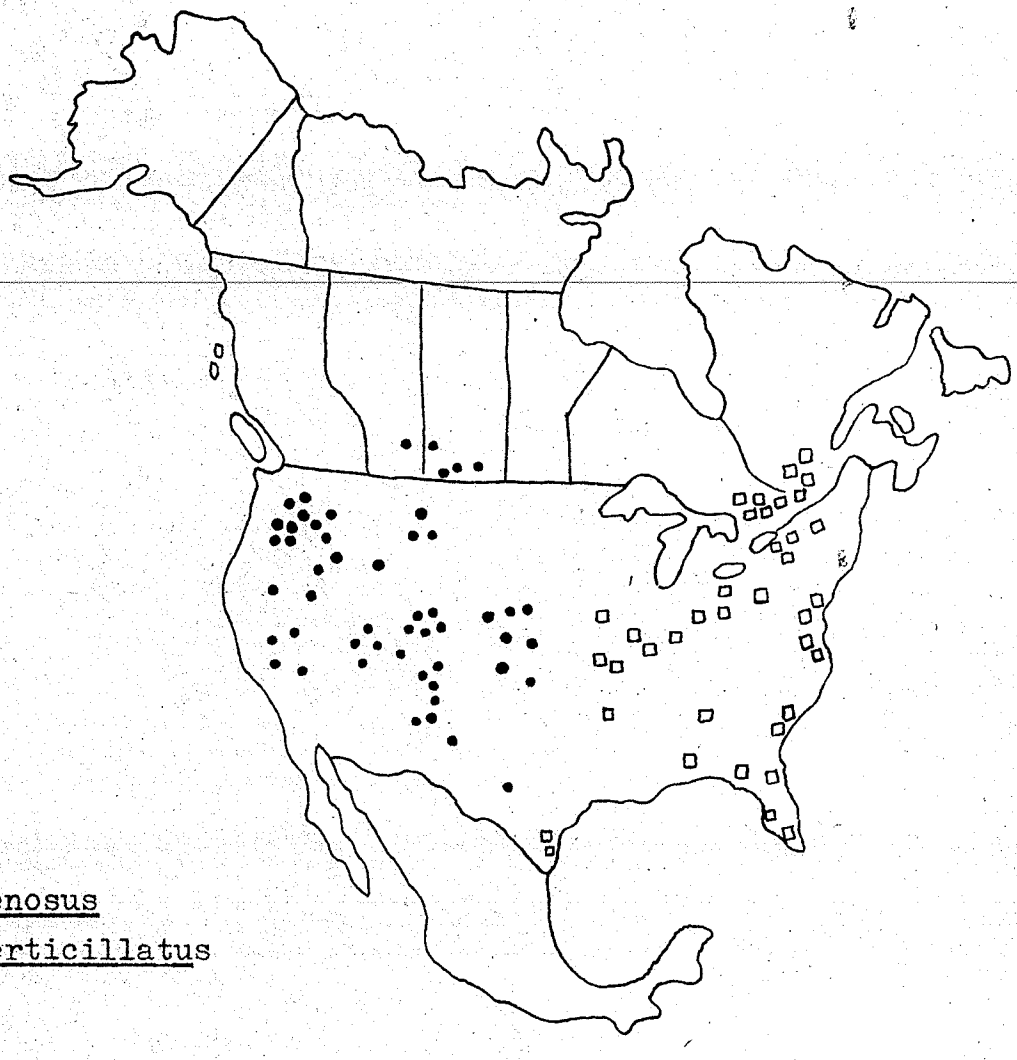


Fig. 1. Distribution of R. venosus and R. verticillatus.

who did not follow Wood's description, giving the measurements of the leaves as up to 20 cm. long and up to 7 cm. broad. Thus it is impossible to determine the valid specific name of the plants investigated here, and they are therefore tentatively referred to as the species R. altissimus until such time as Campdera's and Wood's type specimens are located.

R. utahensis-

Distribution: Rocky Mountains between 36' and 43' N. Latitude. Northwestern United States and Alberta (Fig. 2).

The seeds of the plant investigated here were taken from Sheet No. 113824 from the National Museum of Canada. Although labelled R. altissimus by H.J. Scoggan, this plant is identical in fruiting panicle and valve characteristics, with the plant on Sheet No. 43303 from the same herbarium (collected in Calgary, Alberta), determined by Rechinger as a narrow leaved specimen of R. utahensis. Because of this, it seems justifiable to identify the specimen under present investigation as R. utahensis.

In noting the distribution of this species (Fig. 2), the writer did not include the collection from which the seeds were taken for the present study, as it appears that the species has been introduced to Manitoba.

R. crassus-

Distribution: California, Oregon (Fig. 2).

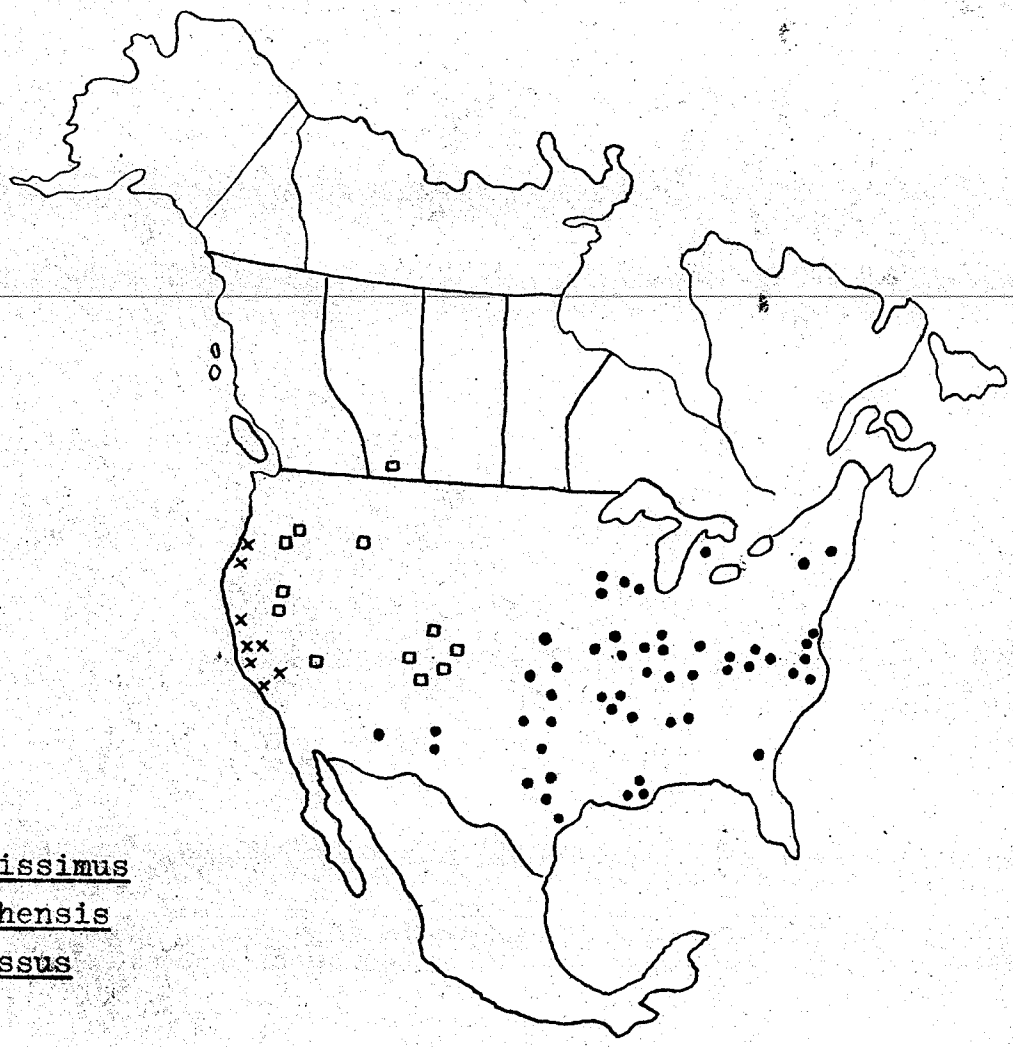


Fig. 2. Distribution of R. altissimus, R. utahensis and R. crassus.

R. transitorius-

Distribution: Rechinger gives the distribution as the Pacific States and Vancouver Island. According to Hulten (1944) the species is also found in Alaska.(Fig. 5).

The seeds of this species were from Vancouver Island. The plants grown from these seeds, although found to differ from Rechinger's original description as to width of leaves and size of grains, were identified as R. transitorius, since Rechinger(1936) includes, under the name R. transitorius, all the Pacific salicifolius - like forms with perigonial segments almost covered by the large grains but never entirely so.

R. pallidus-

Distribution: Eastern Canada, northeastern United States (Fig. 5).

Plants from seeds from two different sources were studied. The plants from the seeds originating in Montreal Botanical Garden agree in all respects with Bigelow's original description of R. pallidus. However the material from the Botanical Garden in Göteborg have leaves which are wider (up to 5.5 mm. broad) and more undulate. These plants also grow more vigorously, producing thicker stems and leaves. This fact as well as the meiotic behavior which is described below, is indicative of a hybrid origin. Figs. 3 & 4 show the differences between R. pallidus proper and the plant of supposed hybrid origin.

Fig. 3. R. pallidus (from Montreal)

(a) plant 1/3 natural size

(b) valve x 3

(c) nutlet x 3

Fig. 4 . R. pallidus (from Göteborg) of supposed hybrid origin.

(a) plant 1/3 natural size

(b) valve x 3

(c) nutlet x 3

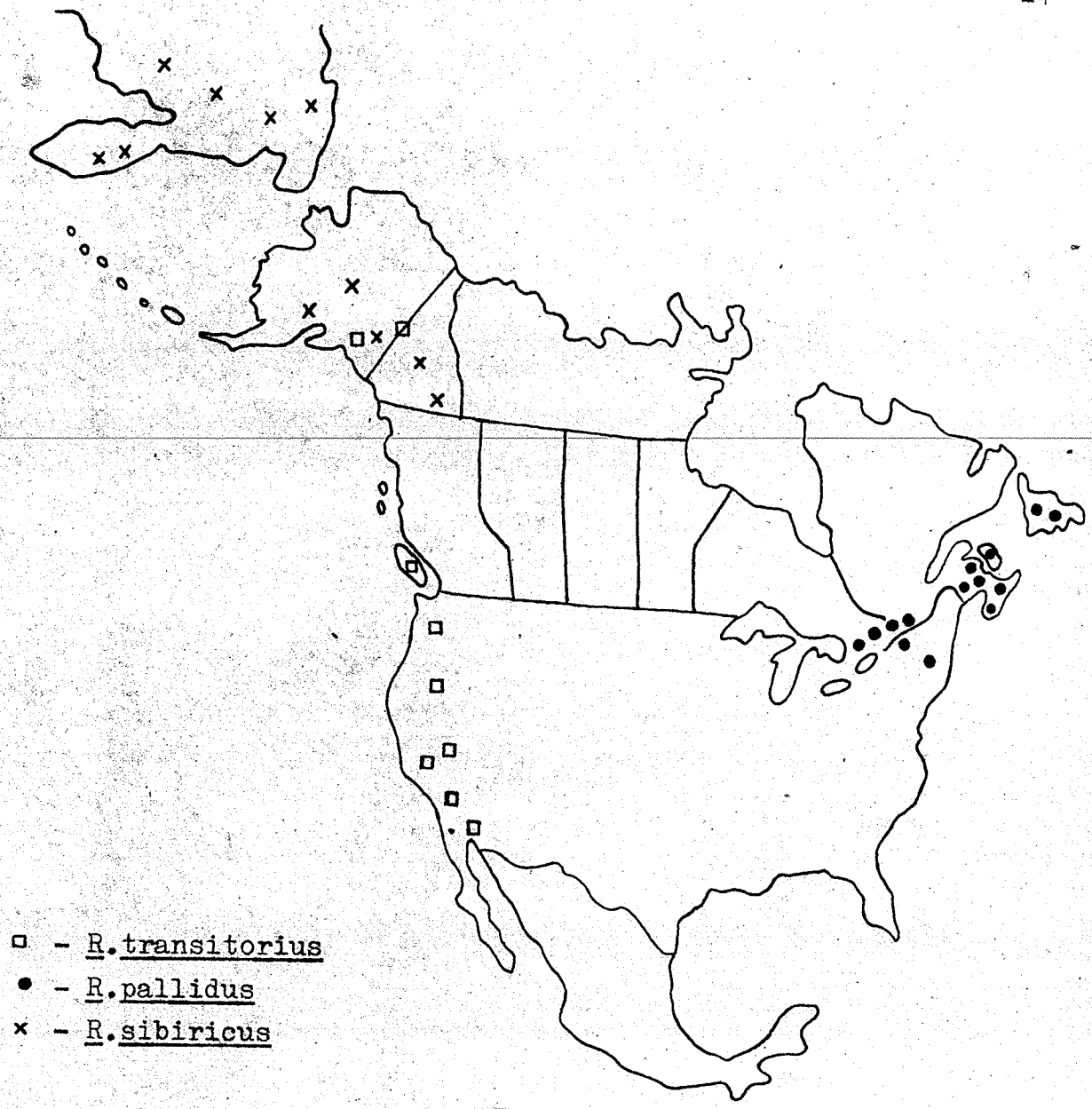


Fig.5 . Distribution of R. transitorius, R. pallidus and R. sibiricus.

R. sibiricus-

Distribution: Northern and eastern Siberia, Kamchatka, Yukon, and Alaska (Fig.5), according to Hulten (1928, 1944).

Although Rechinger gives the distribution of R. sibiricus as extra- American, Hulten(1944) suggests that the plants from Alaska which Rechinger has placed under R. pallidus are actually specimens of R. transitorius and R. sibiricus. From the morphological study of the three species from the different localities, Hulten's decision seems more justified.

R. triangulivalvis-

Distribution: Northeastern, central and western United States, southern Canada (Fig. 6). Introduced to Europe.

R. triangulivalvis is closely related to R. mexicanus, differing only in the size of the fruiting perigonia and the nutlets. These quantitative characters were not considered sufficient by Fernald (1908) to give it a separate status, and he included it under R. mexicanus. Rechinger(1937), however, placed it on a specific level for a rather practical purpose, fully realizing the artificiality of his nomenclature. This move was prompted by a geobotanical consideration rather than a morphological one since R. triangulivalvis differs distinctly from R. mexicanus in its distribution (Fig. 6). R. mexicanus is found only in Mexico and New Mexico, whereas R. triangulivalvis, not found in Mexico, extends fron Mexico northward to Canada. In the opinion of the present writer the separation of the northern forms of R. mexicanus under a specific status, though helpful in delimiting the distributional boundaries of the two types, is

in contradiction to the aim of natural classifications. In the terms of modern biosystematics (Turesson, 1922,1929), R. triangulivalvis would be a geographical ecotype of R. mexicanus, thus warranting a status only up to a subspecific level(Clausen, 1941). It is therefore proposed herein that R. triangulivalvis be recognized as a subspecies of R. mexicanus. It will henceforth, in the present report, be dealt with as:

Rumex mexicanus subsp. triangulivalvis (Danser) Sarkar, comb. nova., based upon R.salicifolius Weinm. subsp. triangulivalvis Danser, Nederl. Kruidk. Archief 415, 1925 (appeared in 1926).

Synonomy: R. triangulivalvis (Dans.) Rech. fil. Repert..Sp. Nov. 40: 297, 1936. R. salicifolius auctorum multorum, non Weinm. R. mexicanus Fernald, Rhodora 10:119, 1908, and Gray's Manual Eighth Ed.:568, 1950, non Meisn. R. mexicanus Gleason, New Britton & Brown 2:69, non Meisn.

The following table shows the differentiating characters between R. mexicanus subsp. mexicanus and R. mexicanus subsp. triangulivalvis. In all other respects, apart from the areas of distribution,the two taxa are identical.

	R. mexicanus subsp. mexicanus	R. mexicanus subsp. triangulivalvis
External perigone leaves	ca. 2 mm. long	1.6 - 1.8 mm. long
Valves	4 - 5 mm. long	(1-)3(-4) mm. long
	3.7 - 4 mm. broad	2.5 - 3 mm. broad
Grains	2.5 - 3 mm. long	1.8 - 2.5 mm. long
	1 mm. broad	0.6 - 0.9 mm. broad
Nutlets	ca.2.5 mm. long	2 mm. long

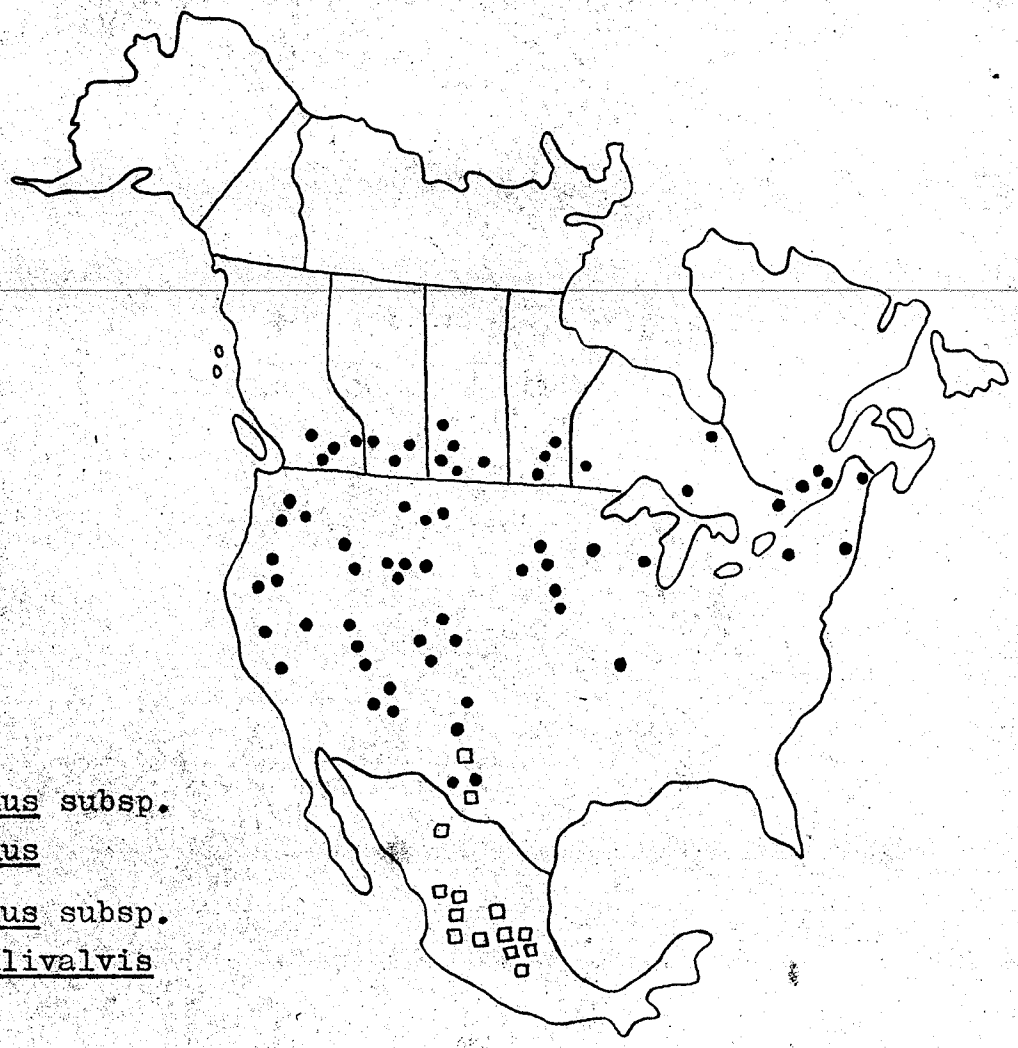


Fig. 6. Distribution of R. mexicanus subsp. mexicanus and R. mexicanus subsp. triangulivalvis.

IV. CYTOLOGY.

1. Mitosis.

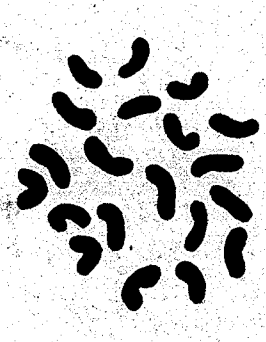
From mitotic studies all the seven species of Salicifolii are found to be diploids with 2n = 20. The one species of Venosi, R. venosus, has 40 somatic chromosomes and is thus a tetraploid. Of the three species in Verticillati, only R. verticillatus has been studied in the present investigation and the somatic number in this species has been found to be 60. The section Axillares thus seems to possess a polyploid series in its subsections.

The subsections are treated separately in the following description of mitosis of the species under consideration here.

Subsection Salicifolii:

1. R. altissimus.

The chromosome number of this species has not been reported previously. The plants upon which the determinations were based were from two Botanical Gardens in Europe. In both cases the number was determined as 2n = 20. The chromosomes possess median or submedian centromeres. They are the largest chromosomes of the Axillares species studied here, their length ranging from 1.44 to 1.86 micra. Fig. 7 shows the somatic metaphase plate of the material from Munich.



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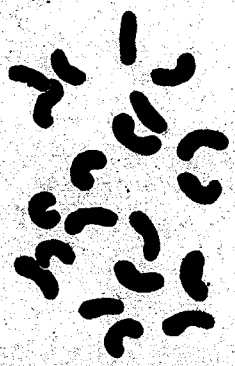

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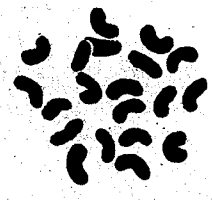

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Figs. 7 - 9. Somatic metaphase plates.- Fig. 7, R. altissimus x 5500; Fig. 8, R. utahensis x 5500 Fig. 9, R. crassus x 4200.

2. R. utahensis.

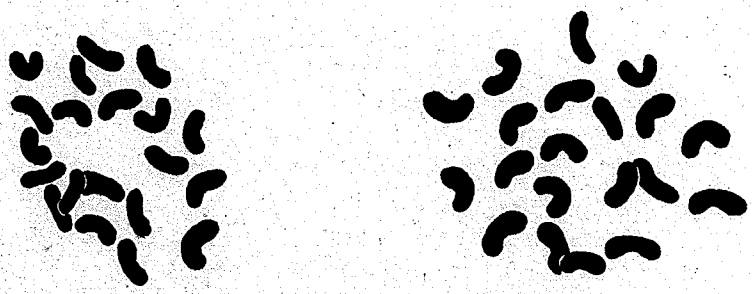
The chromosome number for this species, too, has not been previously reported. The number is found to be 2n = 20, in germinating seeds from a single plant from Grand Rapids, Man. The centromeres are median or submedian. The length of the chromosomes ranges from 1.44 to 1.67 micra. Fig .8 shows a metaphase plate of the species.

3. R. crassus.

This again is the first report of the chromosome number in this species. The number 2n = 20, was determined from germinated seeds from a single Oregon plant. Chromosomes, with median or submedian centromeres, range in length from 1.27 to 1.62 micra. A somatic metaphase plate is shown in Fig. 9.

4. R. pallidus.

Jensen (1936) determined the chromosome number in the pollen mother cells of this species as eight, and as a result the basic number of the Axillares group has been reported as eight. The writer has studied the root tips in R. pallidus proper and in the supposed hybrid, and in both cases the haploid number was shown to be ten. Since in no other species of this group has the haploid number been found to be less than ten, the above mentioned basic number is doubtful.



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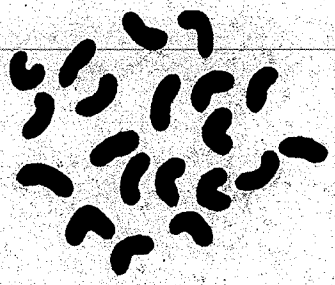
Figs. 10 - 11. Somatic metaphase plates. Fig. 10. R. pallidus (from Montreal) x 5500; Fig. 11. R.pallidus (from Göteborg) of supposed hybrid origin x 5500.

The chromosomes in this species,as in the others, are small, therefore there has been no difficulty in counting due to overlapping of chromosomes in metaphase plates. Figs. 10 & 11 show metaphase plates of material from Montreal and Göteborg respectively. Because of the minute size of the chromosomes, no thorough karyotype study could be made, but the chromosomes are found to possess median or submedian centromeres. The length of the chromosomes ranges from 1.27 to 1.64 micra.

5. R. transitorius.

The chromosome number of this species was not previously determined. The number was found to be 2n = 20. The chromosomes possess median or submedian centromeres. The length of the chromosomes ranges from 1.27 to 1.67 micra with the majority in the larger category. Fig. 12 shows a somatic metaphase plate of the material from Vancouver.



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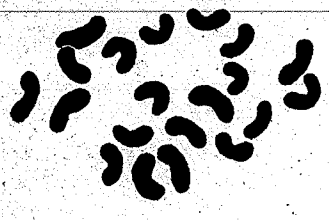

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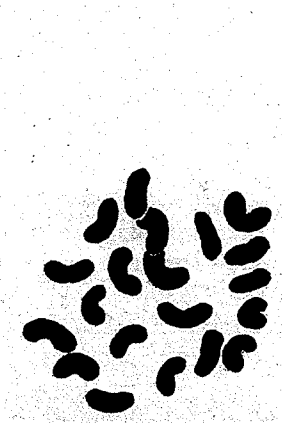
Figs. 12 - 13. Somatic metaphase plates. Fig. 12, R. transitorius; Fig. 13, R. sibiricus . x 5500.

6. R. sibiricus.

This is the first report of the chromosome number of this species. The number 2n = 20, was determined from germinated seeds collected from Dawson, Yukon. Chromosomes, with median or submedian centromeres, range in length from 1.27 to 1.67 micra. A somatic metaphase plate is shown in Fig. 13.

7. R. mexicanus subsp. triangulivalvis.

The chromosome number of this species was not reported previously. The number determined in root tips of materials from nine different sources was in all cases 2n = 20.



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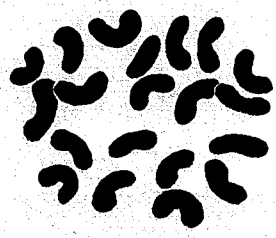

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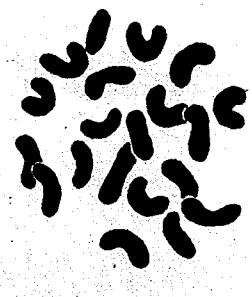

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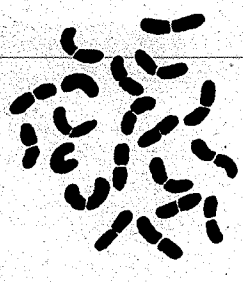

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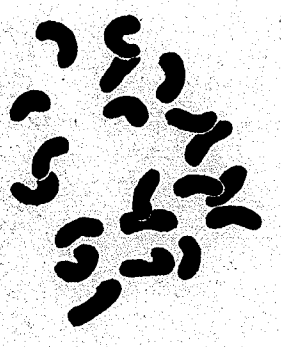

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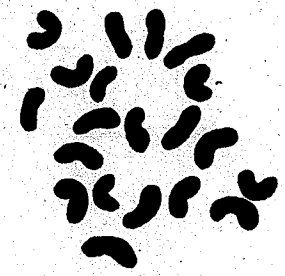

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Figs. 14 - 19. Somatic metaphase plates of R. mexicanus subsp. triangulivalvis. Fig. 14, from Rome; Fig 15, from Ottawa; Fig. 16, from Helsinki; Fig. 17, from Turku; Fig. 18, from Oslo; Fig. 19, from Lund. Magnifications in all cases x 5500.

The length of the chromosomes ranges from 1.10 to 1.67 micra. The centromeres are median or submedian. Figs. 14 to 19 show somatic metaphase plates of materials from different sources. The metaphase plate in Fig. 18 shows distinct centromeres due to the use of Lewitsky's fluid as a fixative. The smaller size of the chromosomes in this plate is also due to the fixative used. For this reason only those plates which had been fixed in Navashin - Karpechenko fixative were compared as to measurements.

Subsection Venosi:

8. R. venosus.

The chromosome number for this species has not been reported previously. The mitotic cells were studied from germinated seeds from two different localities. The chromosome number in both cases was found to be 2n = 40. The length of the chromosomes is the smallest of the Axillares group as a whole, ranging from 0.85 to 1.27 micra. The centromeres are again median or submedian. Fig. 20 shows a somatic metaphase plate of the material from Kindersly, Sask.

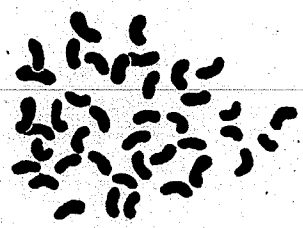

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Fig. 20. Somatic metaphase plate of R. venosus x 4200.

Subsection Verticillati:

9. R. verticillatus.

The chromosome number of this species was given an approximate count by Fink (1899), from observations on the macrospore mother cell during his study of the development of the embryo sac. He found the haploid number of the chromosomes to be approximately 24. This number has been reported as such by Tischler (1927), while Jensen (1936) apparently mistook it for a diploid number.

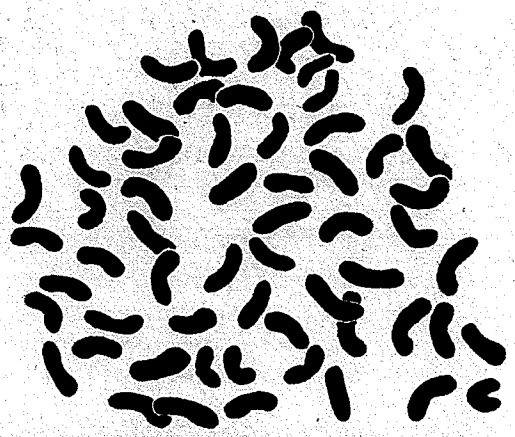

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Fig. 21. Somatic metaphase plate of R. verticillatus x 6000.

In the present investigation the root tips of germinating seeds of this species from three different localities were studied and the somatic number was found to be 2n = 60. The chromosomes have median or submedian centromeres. The length of the chromosomes ranges from 1.27 to 1.86 micra. Fig 21 shows the somatic metaphase plate of this species from Brittania, Ont.

2. Meiosis .

Four species have been studied meiotically, all from the subsection Salicifolii. Studies of the materials from different sources are considered separately.

A peculiarity in the meiotic process was observed in a few of the species. It was found that in some of the pollen mother cells undergoing meiosis usually two, but in some cases only one of the bivalents, instead of its usual configuration, assumed a tripartite appearance. Jensen (1936) had observed some bivalents in R. pallidus to be of this tripartite nature. He, in an attempt to explain this phenomenon, states: "the halves of a meiotic (haploid) chromosome begin to separate and then one of the halves in turn begins to divide, a tripartite chromosome appears to be present." The supposition of a transverse division of one of the chromosomes, however, seems unwarranted, and the usual longitudinal division of one of the chromosomes could hardly give the tripartite structure found both in his diagrams and in the present case.

Tripartite bivalents were observed by Kattermann (1939) in a study of meiosis in inbred rye. He attributed this phenomenon to the presence of an extra terminal centromere in addition to the normal submedian one. Chromosomes with apparent terminal centromeres have been designated by him as T- chromosomes. However, Prakken and Müntzing (1942), also working with highly inbred rye in which the same phenomenon appeared, concluded from interphase plates that the particular chromosomes which exhibited

this phenomenon had only one submedian centromere keeping the chromatids together, so that the attraction of ends of the T-chromosomes to the poles could not be due to a true centromere, at least not in the normal interpretation of the term centromere (Darlington, 1937).

Prakken and Müntzing (l.c.) have found that during the first metaphase, the ends of the short arms of the T-chromosomes are attracted to the poles, while the long arms are held together by one or more chiasmata, so that the bivalent no longer has its typical appearance but assumes a rod-like shape with the ends attenuated into thread-like structures due to strong polar attraction. The two submedian centromeres and the terminal forces work in the same direction and result in the tripartite appearance. Although the separation in metaphase-I is usually normal, difficulties are sometimes encountered due to the formation of a chromatin bridge involving two of the four chromatids.

Prakken and Müntzing conclude that the attraction of the T-end to the nearer pole is conditioned by some special chromosome structure not present in normal lines. At the same time the T-phenomenon is certainly also gene controlled. This phenomenon was exhibited only in the meiotic cells, the mitotic cells from the same plants being normal.

Configurations similar to those which appear in inbred rye have also been observed in some species of Rumex. Because of the much smaller size of the chromosomes, the detail could not be made out as clearly as in rye. However, in some cells the

chromosomes assume the peculiar shape exhibited by T- chromosomes. These , in the present work, will be referred to as T- chromosomes or T-bivalents. At metaphase I, the T-bivalents can be distinguished easily by the tripartite structure which is not to be confused with the presence of two chiasmata, one at each end, in an ordinary bivalent. In normal cases the middle portion of each half of the bivalent is drawn out to a point as might be expected from the normal attraction of the centromere to the pole. However in T-bivalents the ends toward the poles are rounded and the region containing the centromere is evident as a constriction about a quarter of the way, on either side of the bivalent (Fig. 22).

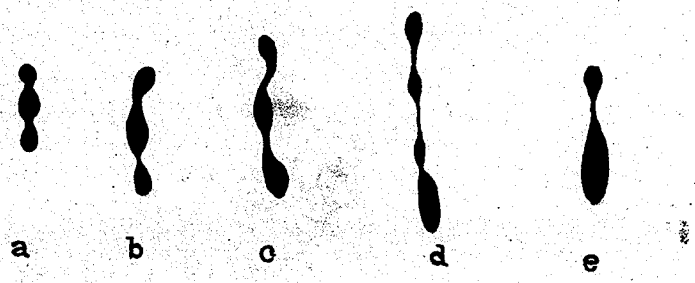

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Fig. 22. T- bivalents drawn separately. a - c, T- bivalents in progressive stages of separation; d, disturbance in separation; e, unequal bivalent. x 3350.

With the beginning of anaphase the T- bivalent becomes drawn out and the centromere region is greatly elongated. The division in spite of these peculiarities appears to proceed

normally and an equal number of chromosomes go to either pole. In a number of cases some disturbances have taken place so that the separating bivalent appears as is shown in Fig. 22,d.

Another phenomenon was observed in some cells. The component chromosomes of a bivalent in some cases were unequal in size (Fig. 22,e). This may perhaps be due to unequal segmental interchange between homologous chromosomes or to heterozygosity regarding the T-chromosome. The phenomenon, whatever its cause, is restricted to the meiotic division since no indication of T-chromosome could be found in any mitotic plates.

The cause of the T- phenomenon is obscure, and Rumex with its minute chromosomes is hardly to be regarded as suitable material for the solution of the problem. But it is interesting that the same observations may be made in such diverse groups as the Gramineae and the Polygonaceae.

Following are the details of meiotic study on the species of Salicifolii.

1. R. altissimus.

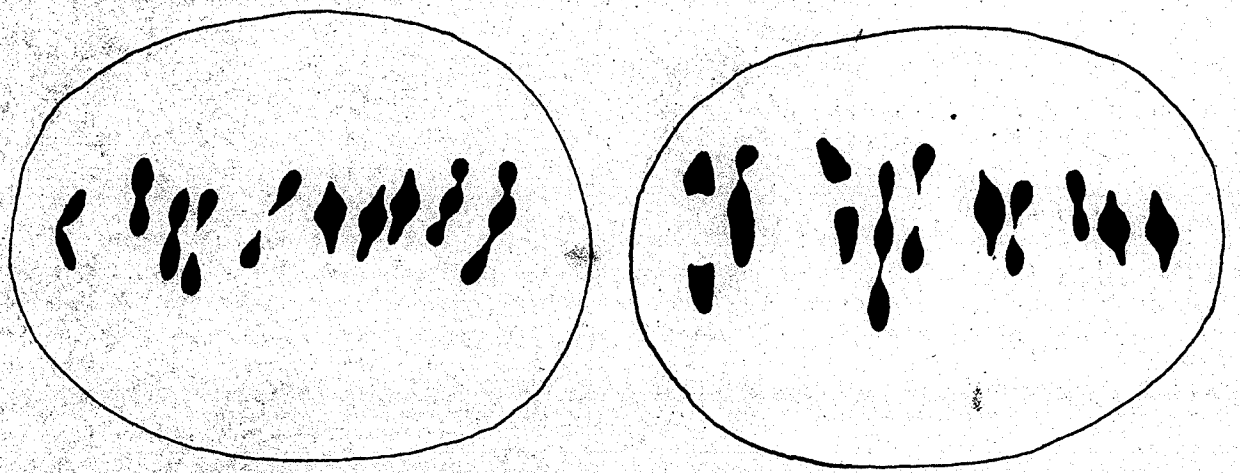
Plants from two different sources were studied meiotically for this species and shall be dealt with separately.

a. From Basel:

This material showed normal meiosis but had by far the largest number of T- bivalents. The number of cells observed for the different stages are as follows:

Configurations	No. of cells.
Metaphase I-normal with 10_{II}	107
Metaphase I- with two T- bivalents.....	16
Metaphase I- with one T- bivalent	28
Metaphase I- with interbivalent connection	1
Anaphase I- normal	10
Total	162 cells.

The number of T- bivalents in this material, though very high, is not consistent in different cells. About 10% of the metaphase cells show the presence of two T-bivalents (Fig. 23), while about 18% show the presence of one T-bivalent (Fig. 24).



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Figs. 23 & 24. Meiosis in R. altissimus from Basel. -Side view metaphase I. - Fig. 23, showing two T-bivalents; Fig. 24, showing one T- and one unequal bivalent. x 3350.

This may be due to different plants from the same source exhibiting varying degrees of the phenomenon since meiosis of individual plants was not recorded separately.

The cause and significance of the interbivalent connection at metaphase I observed in one cell (Fig. 25) are difficult to explain. Thomas and Revell(1946) assumed that connections between bivalents are due to the random fusion of heterochromatic regions. According to their opinion, this phenomenon is responsible for the apparent secondary association of bivalents at metaphase.

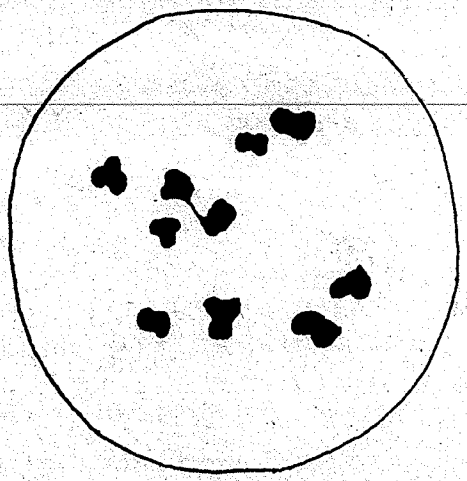

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Fig. 25. Meiosis in R. altissimus from Basel. Polar view metaphase I showing interbivalent connection. x 3350.

b) From Munich.

The configurations seen in meiosis were as follows:

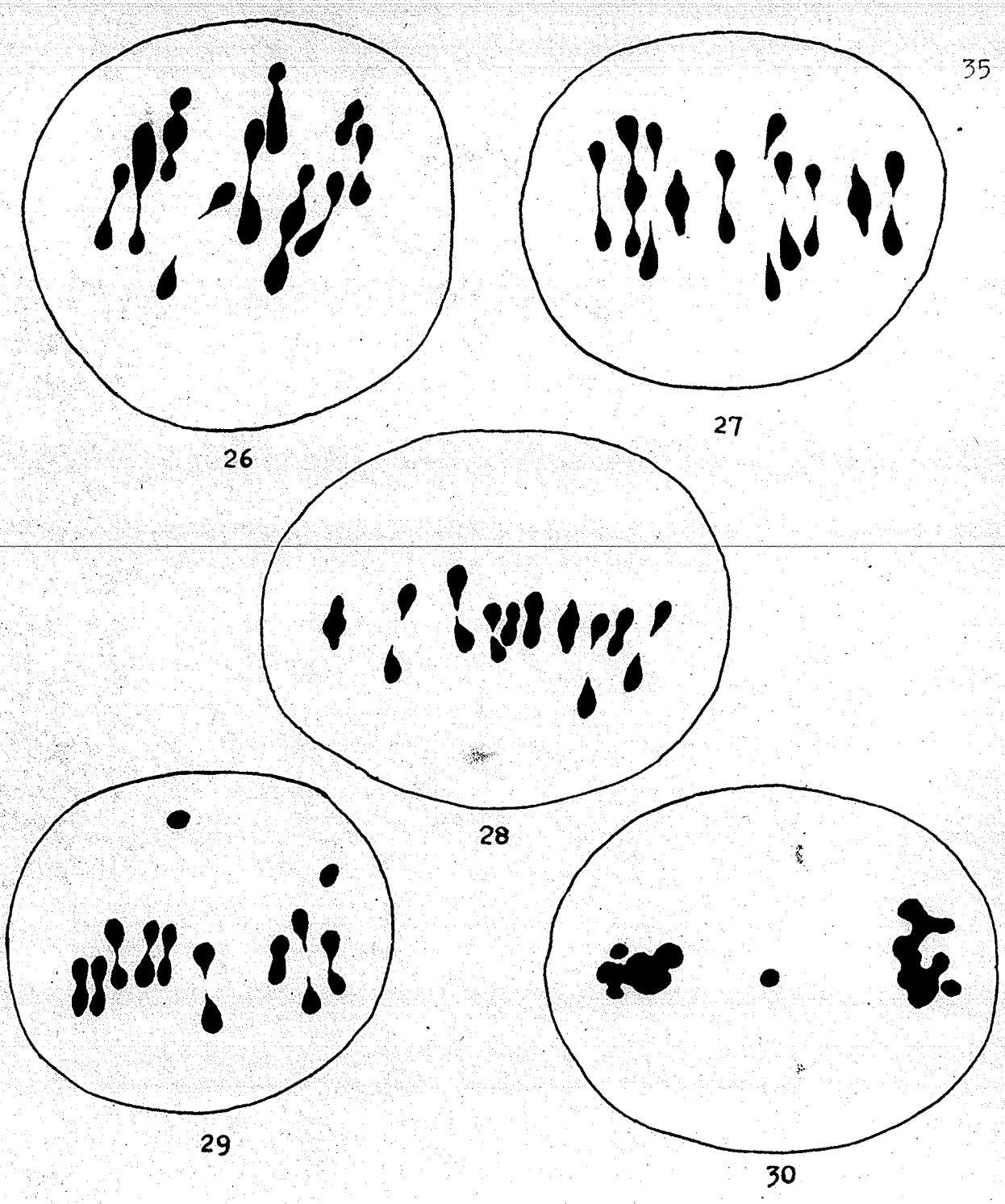
Configurations	No. of cells.
Metaphase I- normal with 10_{II}	152
Metaphase I- with one T-bivalent	4
Metaphase I- with two T-bivalents	3
Metaphase I- with $9_{II} + 2_{I}$	5

Configurations (con't)	No. of cells.
Metaphase I- with two groups of 5 bivalents	4
Anaphase I- normal	20
Anaphase I- with a lagging univalent	1
Total	189 cells.

As may be seen from the above table, the frequency of T-chromosomes is lower in this material than in the preceeding . This is perhaps due to the difference in genetic constitution of the two materials from the different sources and may be compared with races of inbred rye showing different degrees of the phenomenon.(Prakken and Müntzing).

Apart from cells showing T-bivalents(Figs. 26 & 27), occasional metaphase-I cells were observed with bivalents associated in two groups of five. However no interbivalent connections were noticed. The significance of this association is not quite clear and the matter will be considered in the discussion. The presence of univalents in metaphase-I cells (Fig. 29) may be due to heterozygosity for an inversion involving one pair of chromosomes. As most of the bivalents seem to have only one chiasma (Fig. 28), an inversion in the region of chiasma formation would tend to make the two chromosomes fall apart after pachytene, giving the appearance of univalents.

Anaphase-I was found to be generally normal. One cell with a lagging univalent at the equatorial region was however, observed (Fig. 30). The fate of the univalent could not be determined but it can be assumed that either the univalent



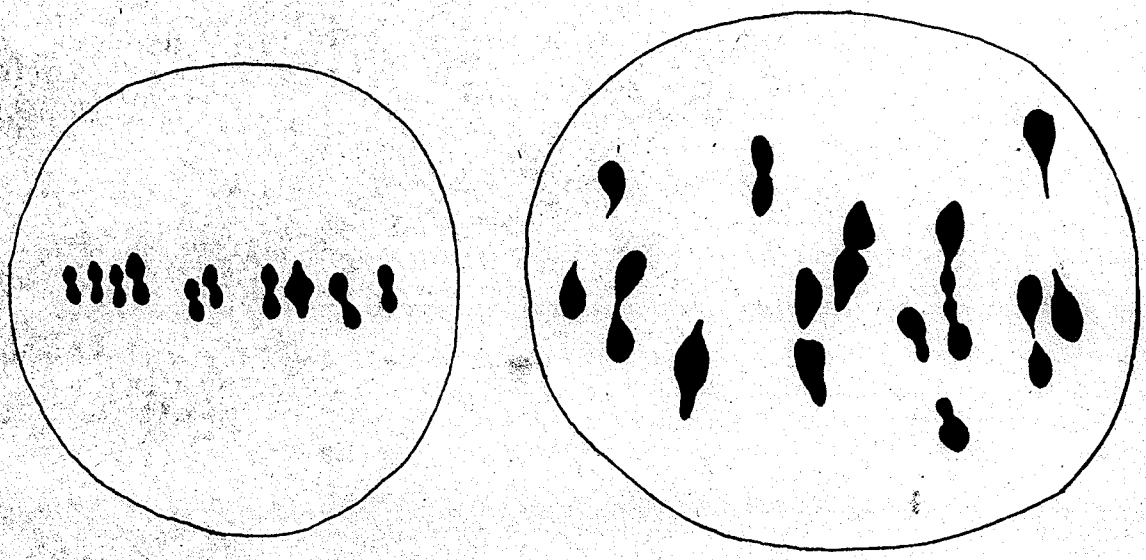
Figs. 26 - 30. Meiosis in R. altissimus from Munich. Side view metaphase-I - Fig.26, with two $T_{\overline{2}}$ and unequal bivalents; Fig. 27, with one T-bivalent; Fig. 28, normal; Fig. 29, with two univalents. -Fig. 30, anaphase-I with a lagging univalent. x 3350.

is included in one of the daughter nuclei, or its split halves go to opposite poles, since no micronucleus was found at interphase.

2. R. pallidus.

a) From Montreal.

This material showed, on the whole, normal meiosis (Fig.31) with the exception of a few instances of T-bivalents (Fig. 32) and univalents.



31 32

Fig 31 - 32. Meiosis in R. pallidus from Montreal. Side view metaphase-I - Fig. 31, normal; Fig. 32, showing one T-bivalent with difficulty in separation. x 3350.

The number of cells with different configurations in metaphase-I together with the number of normal cells seen in anaphase-I are listed below.

Configurations.	No. of cells.
Metaphase-I- normal with 10_{II}	164
Metaphase I- with one T-bivalent	12
Metaphase I- with two T-bivalents	4
Metaphase I- $9_{II} + 2_{I}$	2
Metaphase I- with assoc. of bivalents in two groups of five	5
Anaphase I- normal	10
Total	197 cells.

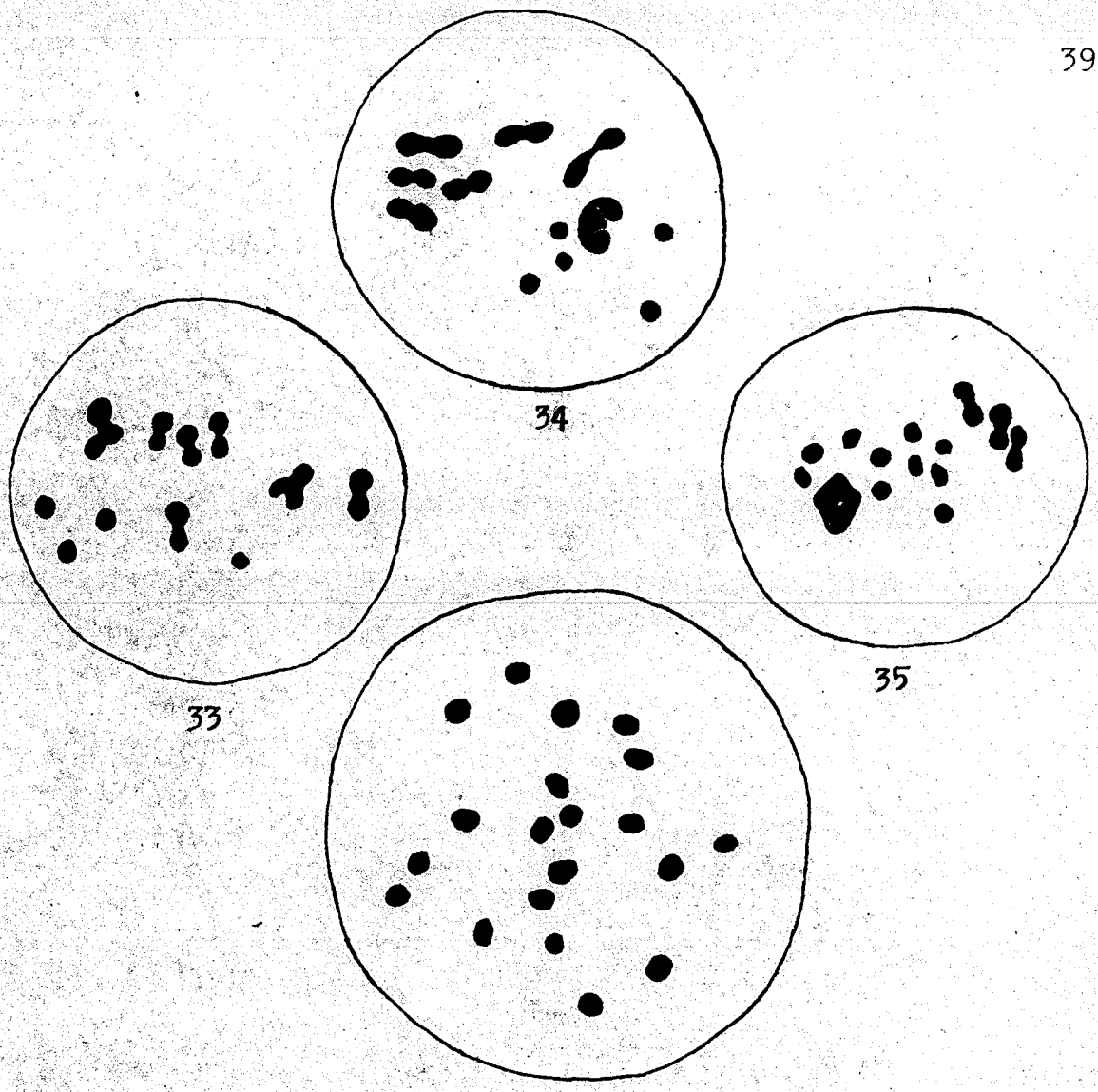
b) From Göteborg.

As formerly stated plants from this source have broader and more undulate leaves than R. pallidus from Montreal. That the frequency of metaphase-I plates with irregular configurations is quite high in this material is shown in the following table.

Configurations.	No. of cells.
Metaphase I- normal with 10_{II}	52
Metaphase I- with one T-bivalent	6
Metaphase I- with 2 groups of 5 bivalents	5
Metaphase I- with 1_{II} off plate	11
Metaphase I- $9_{II} + 2_{I}$	8
Metaphase I- $8_{II} + 1_{III} + 1_{I}$	2
Metaphase I- $8_{II} + 4_{I}$	1
Metaphase I- $7_{II} + 1_{III} + 3_{I}$	1
Metaphase I- $6_{II} + 2_{III} + 2_{I}$	3
Metaphase I- $7_{II} + 6_{I}$	1

Configurations (con't)	No. of cells.
Metaphase I- $6_{II} + 1_{IV} + 1_{III} + 1_{I}$	1
Metaphase I- $6_{II} + 1_{III} + 5_{I}$	1
Metaphase I- $5_{II} + 2_{III} + 4_{I}$	1
Metaphase I- $3_{II} + 1_{II} + 11_{I}$	1
Metaphase I- $3_{II} + 1_{IV} + 10_{I}$	1
Complete asynapsis	2
Total	98 cells.

It is evident from the above that there is a high proportion (24 %) of metaphase-I cells containing univalents. The number of univalents per cell ranges from one to eleven, while two cells showed twenty univalents resulting from complete asynapsis (Fig. 36). This seems to indicate a hybrid origin for the plants concerned. One of the parents must be R. pallidus because of the close resemblance of these plants to R. pallidus proper in regard to the fruiting panicle. The other is probably closely related to it although the decision as to its identity cannot be made at present. The presence of trivalents and quadrivalents in conjunction with univalents (Figs. 33 to 35) in about 12 % of the cells may be due to autosyndesis or segmental interchange, the latter being more likely in consideration of the fact that no tendancy for multivalent formation was noticed in either R. pallidus proper or any other species in this group.



Figs. 33 - 37. Meiosis in R. pallidus from Göteborg (supposed hybrid). Metaphase-I showing- Fig. 33, $4_{II} + 2_{III} + 4_{I}$; Fig. 34, $5_{II} + 1_{III} + 5_{I}$; Fig. 35, $3_{II} + 1_{IV} + 10_{I}$; Fig. 36, complete asynapsis. x 3350.

3. R. transitorius.

The numbers of pollen mother cells with different configurations are given below:

Configurations.	No. of cells.
Diakinesis- normal	12
Metaphase I- normal with 10_{II}	136
Metaphase I- with 1_{II} off plate	10
Metaphase I- with 2_{II} off plate	3
Anaphase I - normal	14
Total	175 cells.

Meiosis in this species is normal (see Figs. 37, 39, & 40) except for a few cases in which one or two bivalents failed to come to the equatorial plate (Fig. 38). This non-congression (Darlington, 1937) is thought to be due to some decrease in the repulsive powers of the centromeres.

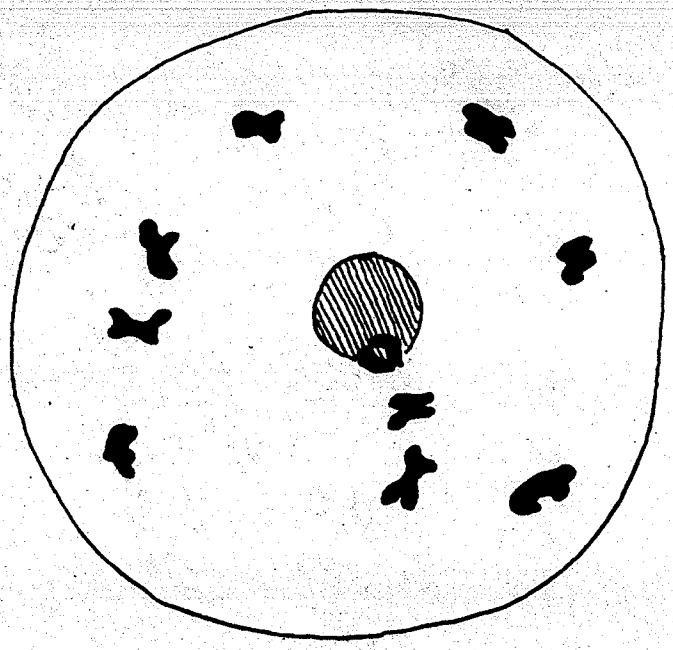
4. R. mexicanus subsp. triangulivalvis.

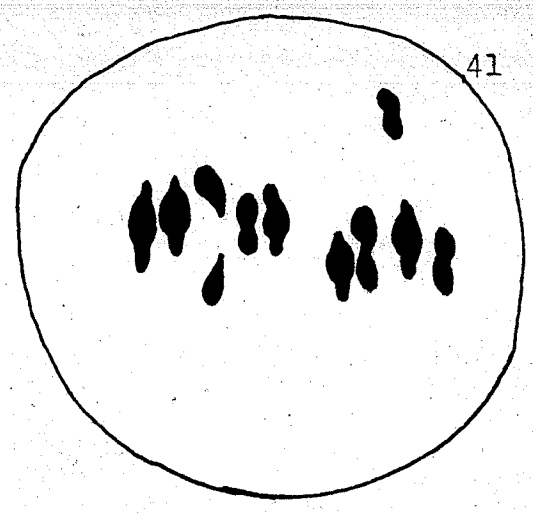
The meiotic behavior of this species was studied in material obtained from five different sources:

a) From Helsinki.

The data gathered from the observations are as follows:

Configurations.	No. of cells.
Metaphase I- normal with 10_{II}	82
Metaphase I- with 2 groups of 5 bivalents.....	7
Metaphase I- with 2 groups of 6 & 4 bivalents...	4
Anaphase I- normal	11
Total	104 cells.





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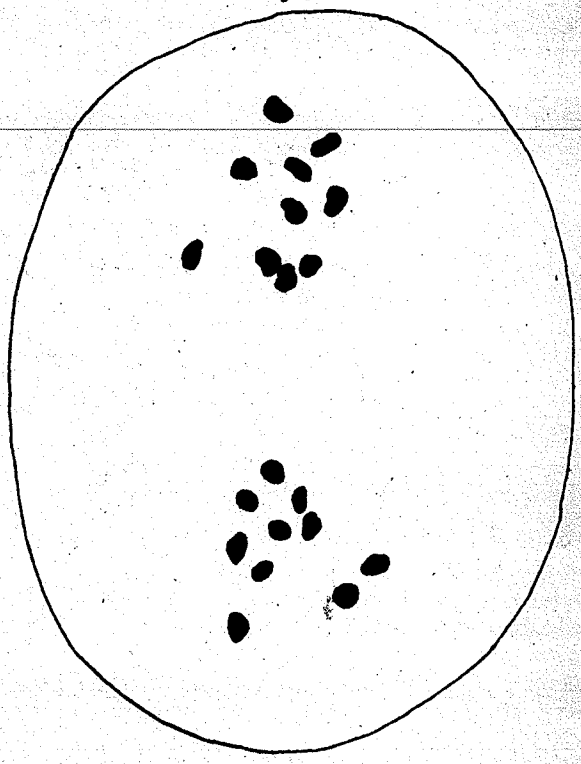

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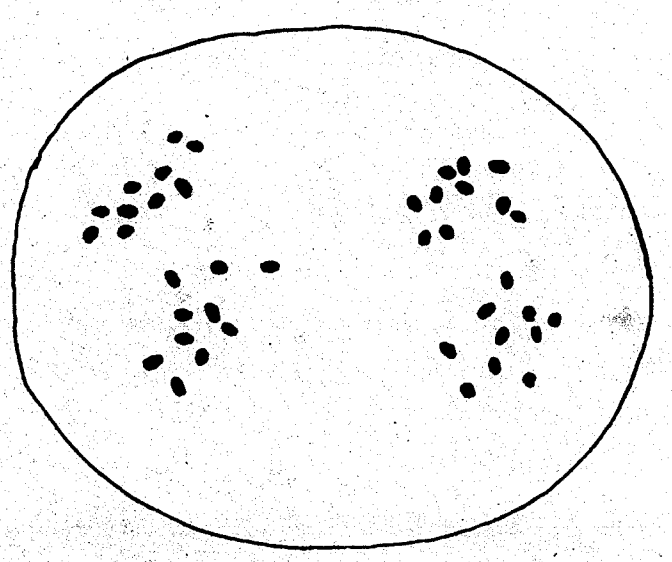

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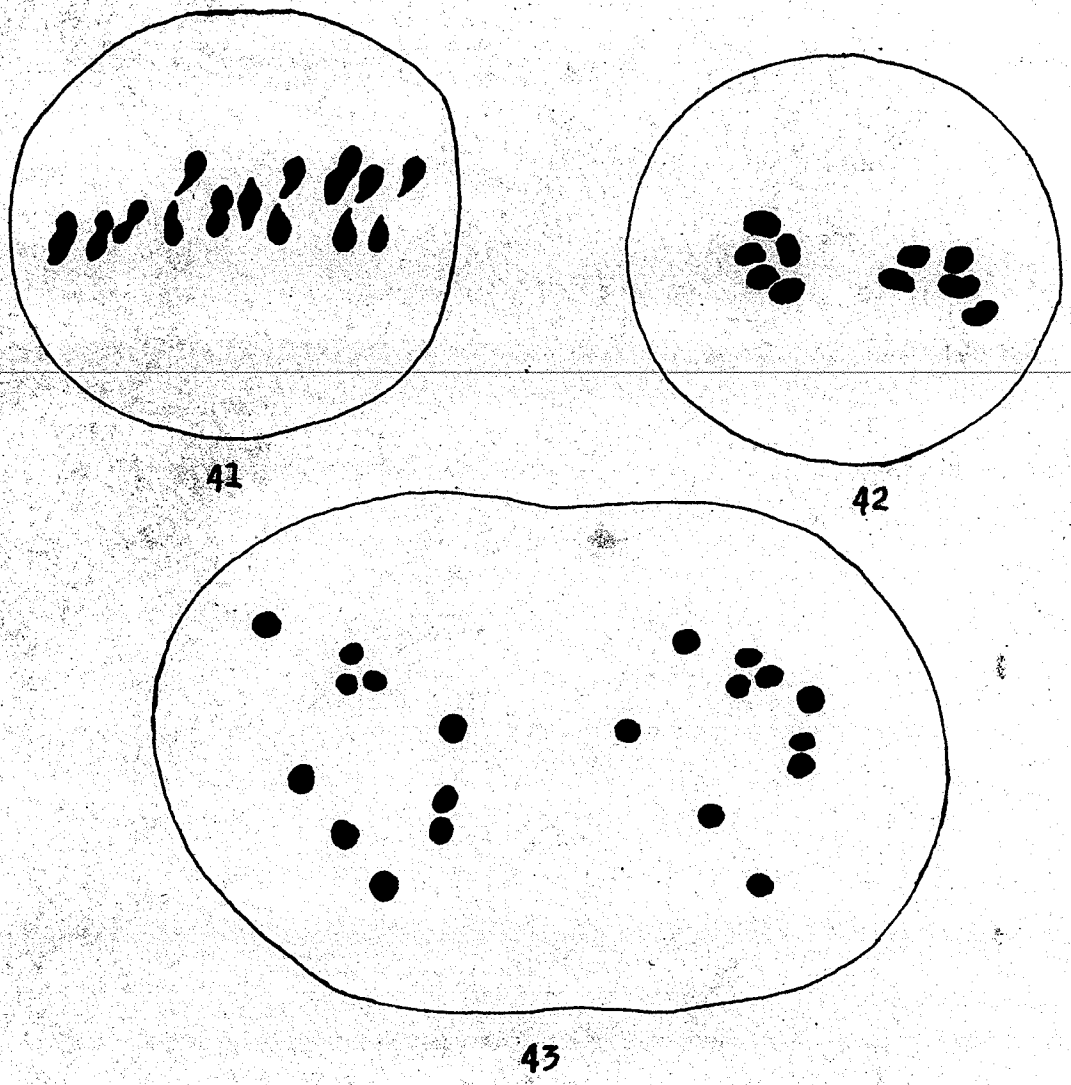
Figs. 37 -40 . Meiosis in R. transitorius

Fig. 37, normal diakinesis with 10_{II}; fig. 38, side view metaphase, with 1_{II} off plate; Fig. 39, normal anaphase-I; Fig. 40, normal anaphase II. x 3350.

Meiosis was found to be normal in this material (Fig. 41 &43) except for a few metaphase I cells showing association of chromosomes in two groups (Fig. 42).



Figs. 41 -43. Meiosis in R. mexicanus subsp. triangulivalvis from Helsinki. Fig. 41, side view metaphase-I with 10_{II}; Fig. 42, polar view metaphase-I with association of 5_{II} + 5_{II}; Fig. 43, normal anaphase-I. x 3350.

b) From Turku.

The following table shows the chromosome configurations for the different stages seen in this material:

Configurations.	No. of cells
Diakinesis - normal	12
Metaphase I - normal with 10_{II}	90
Metaphase I - with 1_{II} off plate	6
Metaphase I - with 2 groups of 5 bivalents..	5
Anaphase I- normal	25
Total	133

As is evident from the above table, meiosis is generally normal with the exception of a few cases of non-congression and association of bivalents in groups.

c) From Lund.

The following table shows the chromosome configurations seen in this material:

Configurations.	No. of cells.
Diakinesis - normal	10
Metaphase I - normal with 10_{II}	99
Metaphase I - with one T- bivalent	3
Anaphase I - normal	15
Total 127 cells.	

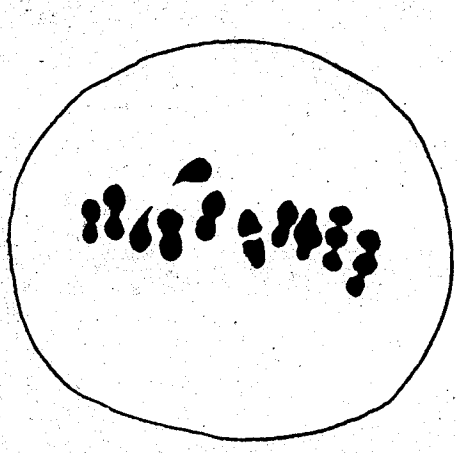
Meiosis is normal in this material except for the presence of T- bivalents in a few cells.

d) From Ottawa.

The following table shows the chromosome configuration in different stages for this material.

Configurations.	No. of cells.
Diakinesis - normal	15
Metaphase I - normal with 10_{II}	175
Metaphase I - with $9_{II} + 2_{I}$	5
Metaphase I - with 1_{II} off plate	8
Metaphase I - with 2_{II} off plate	2
Metaphase I - with two T- bivalents	4
Metaphase I - with 2 groups of 3 bivalents and 2 groups of 2 bivalents	1
Metaphase I - with 2 groups of 5 bivalents	15
Anaphase I - normal	15
Total	244 cells.

As is evident from the above table meiosis is generally normal in this case as well. However metaphase-I cells with clear T-bivalents have been observed (Fig. 44). Non- congression of one or two bivalents is also quite frequent (Fig. 45). The presence of two univalents (Fig. 46 & 47) can be explained in the same manner as for R. altissimus. Apart from these irregularities, there were also cells with two groups of five bivalents (Fig. 48); and in one cell two groups of three bivalents and two groups of two bivalents were observed (Fig. 49)



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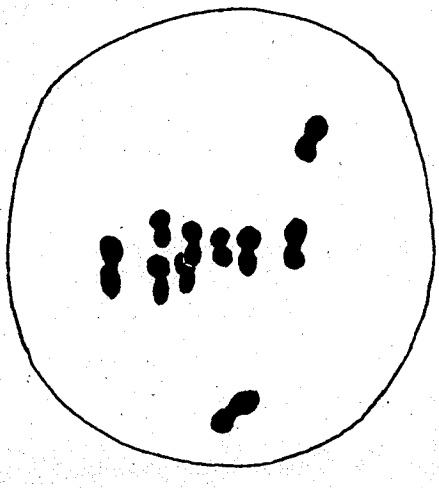

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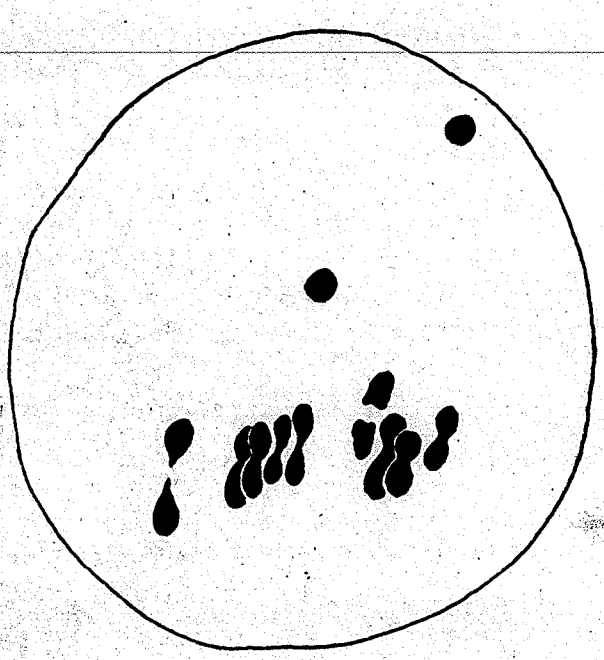

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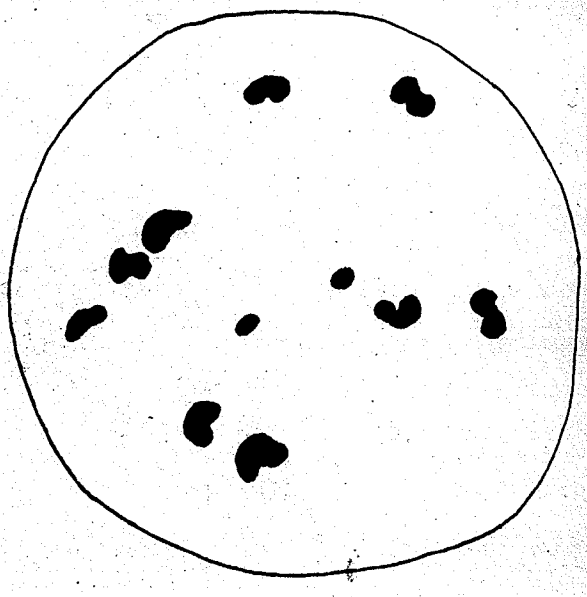

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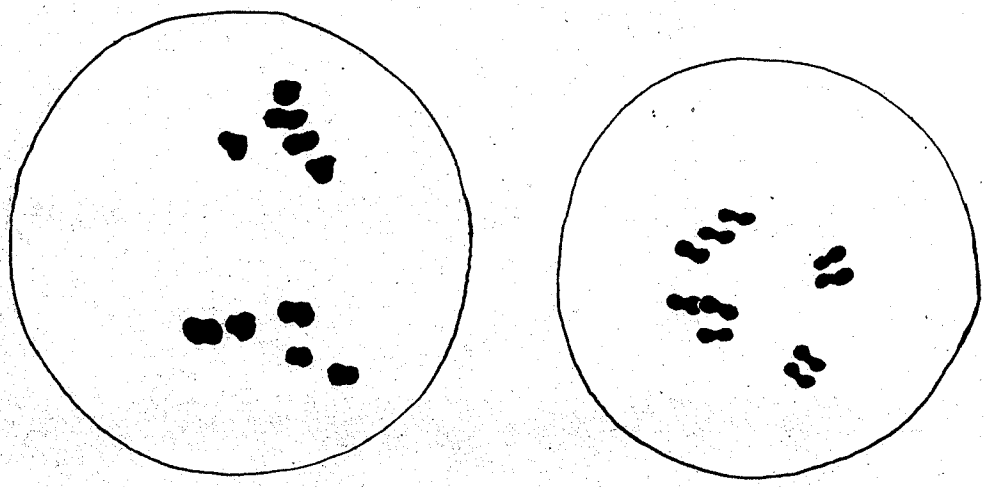
Figs. 44 - 47. Meiosis in R. mexicanus subsp. triangulivalvis. Side view metaphase-I showing- Fig. 44, two T- bivalents; Fig. 45, non- congression of two bivalents; Fig. 46, $9_{II} + 2_{I}$. Fig. 47, polar view metaphase with $9_{II} + 2_{II}$. x 3350.



48 49

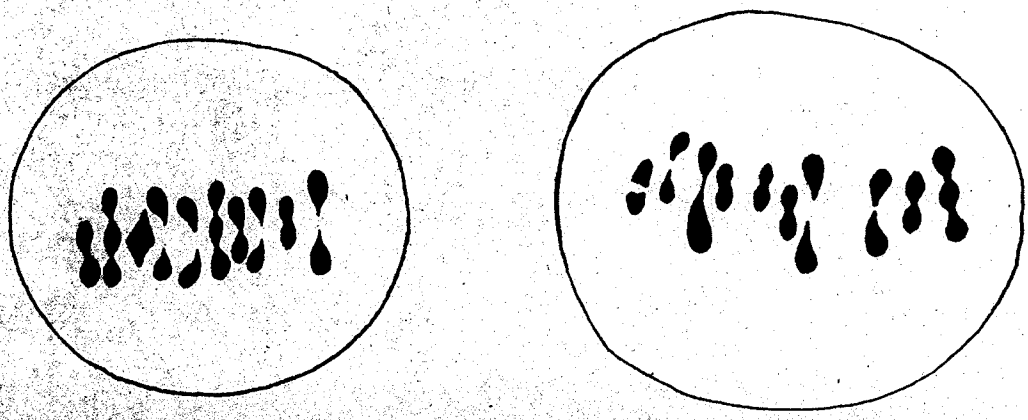
Figs. 48 & 49. Meiosis in R. mexicanus subsp. triangulivalvis. Metaphase-I showing - Fig. 48, association of bivalents in two groups of five; Fig. 49, association of bivalents in two groups of three and two groups of two. x 3350.

e) From Oslo.

The number of cells seen in the different stages for this material are given below:

Configurations.	No. of cells.
Metaphase I- normal with 10_{II}	119
Metaphase I- with one T- bivalent	3
Metaphase I- with two T- bivalents	5
Metaphase I- with 1_{II} off plate	4
Anaphase I- normal	25
Total	156 cells.

As is evident from the above table meiosis is usually normal in this material. However T-bivalents do occur



50 51

Figs. 50 & 51. Meiosis in R. mexicanus subsp. triangulivalvis from Oslo. - Showing side view metaphase - Fig. 50, with two T- bivalents; Fig. 51, with one T- and one unequal bivalent. x 3350.

occasionally (Fig. 50). In one plant the configuration of one of the two T- bivalents seems to indicate that the plant concerned is heterozygous for one T- chromosome. (Fig. 51).

f) From Rome.

The number of cells for the different stages seen in this material is as follows:

Configurations.	No. of cells.
Diakinesis- normal	12
Metaphase I- normal with 10_{II}	133
Metaphase I- with one T-bivalent	12
Anaphase I- normal	15
Total	172 cells.

Meiosis in this material, apart from somewhat high frequency of T- bivalents, is normal.

V. DISCUSSION.

The three subgenera of Rumex are morphologically and cytologically clearly distinguishable. No successful cross between members of different subgenera has yet been reported, either naturally or experimentally. According to Löve(1940), there are great differences in the size of the chromosomes between the subgenus Acetosa on the one hand, and the two other subgenera Acetosella and Lapathum on the other. The diploid species of Acetosa and Acetosella have been found to include differences in karyotype, while in the diploid species of Lapathum no clear evidence for such differences has yet been found. Acetosella and Lapathum have been found to differ from Acetosa in the frequency of polyploidy, which is almost unknown in Acetosa but is very common in both the other subgenera. Löve (1943) postulated that the three subgenera may have developed from a common ancestor as three different but parallel lines of evolution. Further, according to him, the differentiation in species in the subgenus Lapathum is due mainly to alloploidy, while the differentiation of species in the subgenus Acetosella is due solely to autoploidy. This is in accord with the opinions of Kihara and Ono (1926), and Jaretzky (1928) that hybridization has been largely responsible for polyploidy in the subgenus Lapathum.

However, Rechinger (1949), in showing the difference in genetic behavior between the sections Simplices and Axillares states that while the members of the former section cross

easily with each other and some also with those of Axillares, there is no case of hybridization known within the Axillares. The individuals of supposed hybrid origin reported under R. pallidus in the present investigation, do not necessarily invalidate the above contention, but show that occasional hybridization is not impossible.

All the species taken under consideration in the present study belong to the section Axillares, whose principle area of distribution and probably most important centre of evolutionary development is in North America (Rechinger, 1937). Of the eighteen North American species of Axillares, fourteen species are in subsection Salicifolii, three in Verticillati, and only one in Venosi. All the seven species of Salicifolii studied here were found to have 20 somatic chromosomes. R. salicifolius, the only member of this group for which the chromosome number has been recorded, has also been reported to have the somatic number, 2n = 20 (Kihara and Ono, 1926; Jaretzky, 1928). Though no thorough karyotype study was made here, the chromosomes were seen to have median or submedian centromeres. The range of the chromosome length is approximately the same in all the seven species and no noticeable difference in the basic type of chromosome could be distinguished in the different species of this group. The consistency of chromosome number finds corroboration in the morphological conformity of different species.

The single species of the section Verticillati studied here is R. verticillatus. This species is remarkably similar in

gross morphology to the species of Salicifolii, differing only in the considerably longer length of its pedicels. In this species the pedicels are arranged in whorls, while R. fascicularis and R. floridanus, the remaining members of this subsection, do not share this character but are placed in this subsection because of the comparable length of their pedicels. R. verticillatus has been found to have 60 somatic chromosomes. The range in length of the chromosomes is the same as in the subsection Salicifolii and the centromeres are also median or submedian. This similarity in chromosome length together with the close morphological similarity may indicate a derivation of this species from some species of Salicifolii through autoploidy. This hypothesis, though probable, needs confirmation from meiotic studies of this species.

The monotypic subsection Venosi, represented by R. venosus, has been found in the present study, to have 40 somatic chromosomes. Morphologically this species is distinguished from all others of the section Axillares by its remarkably large grainless valves and the large size of its nutlets, though it shares the characteristic of axillary growth with the rest of the species of Axillares. The chromosomes in this species are shorter than those of other species in the section. However there is an overlapping in the range of chromosome length, indicating that in the chromosome set of R. venosus, some chromosomes may have come from a diploid species of Salicifolii, while there are some whose origin must be looked for elsewhere. It is here

assumed that R. venosus is of allopolyploid derivation. One of the parental species involved is perhaps a member of Salicifolii, while the identity of the other species is difficult to ascertain at the present time. That the exceptional size of the valves cannot be accounted for by merely an increase in chromosome number is evidenced by R. verticillatus where the hexaploid nature makes little difference in the size of the valves.

The need for taxonomical separation of polyplotypes as distinct species has been reemphasized in recent times by Valentine (1950) and Löve (1951). The latter author (1943) and Löve and Löve (1942) raised doubt regarding the existence of any polyploid series without some taxonomically noticeable differences. The section Axillares studied here, provides a very good example of the existence of taxa with only slight morphological differences, but having different chromosome numbers. The division of Axillares into three subsections had been made on a morphological basis without a knowledge of the chromosome number of the constituent species of each group. The detection of a polyploid series in this group in the present investigation supports the earlier decision from the morphological point of view, and the degrees of polyploidy correspond with the different subsections.

The subgenus Lapathum seems to be characterized by different basic numbers. The monotypic section, Platypodium, has eight haploid chromosomes reported for its species R. bucephalophorus (Kihara and Ono, 1926; Jaretzky, 1927). The basic

number for the section Simplices has been reported as 10 by Löve (1943). Datta (1952) has, however, proposed 9 as the basic number in this group from the evidence of secondary association in R. dentatus.

Darlington (1928, 1932), Darlington and Moffett (1930), and Moffett (1931) were the first workers to report secondary association as an indication of residual attraction between chromosomes phylogenetically related to each other. Thus, this phenomenon is thought to be intimately connected with alloploidy (Lawrence , 1931) and has been used as a measure of long established phylogenetic relationship between the chromosomes present in a polyploid (Müntzing, 1933; Catcheside, 1934; Nandi, 1936 and others). The significance of secondary association as an indication of relationship of chromosomes has, however , been questioned by many authors. Helm (1934) gave a purely mechanical interpretation of secondary association which has been supported and elaborated by Heilborn (1937). According to these authors, the so-called secondary association is due mainly to a sorting effect of the forces of nuclear division upon chromosomes of different size and mass. Thomas and Revell (1946) concluded that the apparent secondary association is due to random fusion between heterochromatic regions of the chromosomes and has no phylogenetic significance.

It is obvious from the diversity of opinions on the subject, that conclusions should be drawn with great care from the phenomenon of secondary association. Datta's (1952) evidence

has been carefully studied in this light. The frequency of maximum association of chromosomes in nine groups seems to be too low in R. dentatus to make a decision regarding the basic number of the Simplices group as a whole. The association of bivalents found in the present investigation, in several species, is too infrequent and inconsistent to indicate any definite secondary polyploidy in this group.

Löve (1943) has reported the basic number of the section Axillares as eight, apparently from the chromosome number (2n = 16) reported by Jensen (1936) for R. pallidus. It is however evident, from the results obtained in the present investigation, in which 2n = 20 for all the diploid species studied in subsection Salicifolii, and the consistent multiples of 10 in the subsections Venosi and Verticillati, that the basic number of the Axillares group is ten. This is in accordance with the postulation by Winge (1917) that when groups of species have chromosome numbers in a series of multiples of a common number and the chromosomes are of similar form, these species are probably derived from forms with this "basic number" by polyploidy.

SUMMARY.

1. The Axillares section of Rumex subgenus Lapathum was found to contain a polyploid series, the degree of ploidy corresponding with the three subsections.

2. Each of the species studied in the subsection Salicifolii was found to have 2n = 20.

3. The monotypic subsection Venosi is represented by R. venosus with 2n = 40. From chromosome size and gross morphology, an alloploid derivation of this species has been suggested.

4. Of the three species in subsection Verticillati, one, viz., R. verticillatus was studied meitotically and was found to have 2n = 60. An autoploid derivation of this species has been postulated.

5. Meiosis has been studied in the following four species of Salicifolii: R. altissimus, R. pallidus, R. transitorius, and R. mexicanus subsp. triangulivalvis. Meiosis was found to be generally normal.

6. Tripartite bivalents were found in a few of the species which have been thought to be analogous to T- chromosomes in inbred rye (Kattermann, 1939; Prakken and Müntzing, 1942).

7. Plants of R. pallidus from seeds obtained from Göteborg, Sweden showed irregularities in meiosis indicating a hybrid origin.

8. From the consistent haploid chromosome number of 10 and its multiples, the basic number of the Axillares is believed to be ten.

9. Because of the similarity in morphology but difference in distribution between R. mexicanus and R. triangulivalvis, the latter taxon has been reclassified as R. mexicanus subsp. triangulivalvis.

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