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Scottish Plant Breeding Station, Pentlandfield

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SCOTTISH PLANT BREEDING STATION
PENTLANDFIELD, ROSLIN, MIDLOTHIAN

RECORD

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Scottish Plant Breeding Station

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Chief Assistant	W. Black, Ph.D., D.Sc., F.R.S.E.
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	Miss A. R. Hutchison, B.Sc.
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	W. Brown
	Mrs A. W. Chatham
	Miss R. Cruickshank
	Miss W. Sommerville
	A. Young
	Miss J. McMillan
Secretary	R. J. L. Gallie, F.C.C.S.
Assistant Secretary	Miss A. Malcolm.
Clerical Officer	Miss A. G. Dunnett.
	Mrs H. H. Gray (*resigned*).
Clerical Assistant	Mrs I. Blyth.
Shorthand Typist	Miss R. Jackson.

DIRECTOR'S REPORT

Brassica Crops.—Autotetraploids are increasingly being used in the breeding programme and for this reason their cytological behaviour in so far as it affects fertility is a matter of much interest. In spite of a fairly low quadrivalent frequency (about 1·5 per cell) occasional aneuploids have been detected in C_1 generation autotetraploid *B. oleracea* ($2n = 36$) grown under greenhouse conditions. Although the majority of plants were normal individuals with $2n = 35$, $2n = 37$ and one plant with $2n = 34$ were found. Meiosis in aneuploids was naturally abnormal and an especially high incidence of univalents was observed. Selection for fertility and vigour in autotetraploid populations should greatly reduce or eliminate aneuploids in succeeding generations. These observations emphasise the futility of comparing very raw autotetraploids with their corresponding diploids in field trials. Autotetraploids of thousand-headed kale selected on the basis of their performance in the field have been seeded in insect-proof cages containing blow-fly pollinators, and those plants producing the highest seed yields under polycross conditions have been chosen to form the basis of the next generation: already the fertility of some of them appears to be quite high (approximately ten seeds per siliqua) and could no doubt be further improved by selection.

Several thousand interspecific crosses between *B. oleracea* and *B. campestris* have been carried out, all at the tetraploid level. In nearly all cases *B oleracea* was used as the female parent, its flowers being larger and easier to emasculate. Different forms of the parent species were used in the hope of obtaining new amphidiploids. The cross between *B. oleracea* and *B. campestris* is difficult to effect, the normal expectancy being in the order of one seed per thousand pollinations. One of the barriers to crossing is in the style where foreign pollen tends to be extremely slow growing, as a consequence many embryo sacs abort before fertilisation can be affected.

Crosses were attempted by injecting pollen direct into the ovary region. This intra-ovarian pollination technique was used principally on diploid material. Only a very small number of seeds was produced and no true hybrids resulted. Growth substances have occasionally been successful in other genera both in stimulating pollen-tube growth rate and in preventing premature abscission of the ovary with subsequent improved seed setting. The auxins 1 naphthyl-acetic acid, 2 naphthoxy-acetic acid and indole-acetic acid, as well as boric acid, were used in attempts to produce hybrids in greater numbers. Three methods of application were tried (*a*) auxin injected into each pedicel, (*b*) auxin run in around the base of the ovary, (*c*) cotton wool soaked in auxin tied round the peduncle at the time of pollination. Control pollinations using the same pollen on the same female plant but without growth substance were also performed. There was no enhanced effect of auxin in terms of seed set or in the number of ovaries stimulated (*i.e.*, not abscissed). The majority of the small number of seeds obtained gave rise to maternal plants.

Incompatibility between endosperm and embryo in interspecific crosses appears to lead to embryo abortion. Embryos from such crosses had not progressed beyond the heart-shaped stage (*i.e.*, with cotyledons just differentiated) at three weeks after pollination. In compatible crosses this stage is normally reached after about ten days. A greater number of hybrids might be raised by excising embryos and growing them *in vitro*. This is being attempted.

Crossing within *B. oleracea* in an attempt to produce new low growing forms suitable for grazing have involved combinations of thousand-headed kale with kohl-rabi, cabbage and broccoli. Ordinary thousand-headed kale, ' Canson ' kale and three cultivars of curly kale (one of them a tetraploid obtained from Svalöf) were compared with particular emphasis on the amount of leaf lamina produced, this being the high protein constituent of the plant and the part most readily acceptable by the grazing animal. ' Canson ' and ordinary thousand-headed kale showed no significant differences in respect of total leaf dry-matter or of leaf lamina. ' Canson ' yielded about 50 per cent less stem. The two diploid curly kales did not differ significantly from ' Canson ' in respect of total leaf dry-matter but the amount of leaf lamina produced was considerably greater. The tetraploid was of a dwarf strain and was low in total dry-matter (stem plus leaf) but yielded as much leaf lamina as ' Canson '. The experiments were carried out on spaced plants.

In club-root tests both 2x and 4x cultivars of turnip rape (*B. campestris*) were shown to be highly susceptible to a local strain of *Plasmodiophora*. *B. campestris* ssp. *rapifera* 'Gelria', an entire-leaved turnip, exhibited no club-root symptoms when subjected to the same strain and spore concentration. F_2 hybrids between 'Gelria' and ssp. *nipposinica* (highly susceptible) showed continuous segregation which suggests that resistance is polygenic.

In response to the growing demand for swede cultivars capable of being mechanically harvested with the minimum of waste, 'Pentland Harvester', an early maturing swede with an erect and uniform growth-habit, was introduced last year. At the same time as 'Pentland Harvester' was being developed efforts were being made to obtain lines of equal uniformity and of reasonable cropping capacity in the mid-season maturity class. One of the most promising of these lines has been multiplied on a small scale and will be undergoing preliminary harvesting trials in the autumn of this year and more extended trials in 1964.

Genecology and Herbage Plants.—While some hill areas may be known as grassy hills, others as heathery hills, rough grazings especially on the upper slopes are generally composed of a mosaic of plant communities related to the edaphic conditions. It has been shown that whilst all communities are grazed at some season of the year, there are marked differences in the amount of grazing each community receives. Therefore, a logical method of improving conditions would be to increase the number of communities containing the most valuable constituents, and to step up their yield or quality potentialities while still retaining the general pattern of hill vegetation. Basically, the problem as far as the open hill is concerned is the creation, or extension of habitats capable of supporting the more nutritious native species and the understanding of the capacity of these species to respond to specific treatments. Thus the hill land investigations now in progress are primarily concerned with the details of habitat development and habitat-plant population interrelationships, and in particular with the factors which influence the local distribution of species and of intraspecific variation.

For example, a detailed study of these factors is being carried out on the "flushed" area mentioned in the Record for 1962 since an area of this type provides useful gradients in respect of a number of environmental factors. Considerable emphasis has been placed on the investigation of soils both in this area and elsewhere on hill land, the soils varying from wet and coarsely sandy with a high pH, through moist brown earths of moderate pH, to shallow podsols with a deep acid humus layer. The question of how best to express nutrient levels in terms equally meaningful for such a wide range of soils has been given particular attention, for it is considered unsatisfactory to express the mineral status in terms of absolute amounts of exchangeable nutrients. This is particularly true of soils of different humus content which give values for exchangeable ions inconsistent with the pH. It is considered that cation exchange capacity is the most significant variable and this has been determined for all soils. Exchangeable cations have been expressed as a percentage of the cation exchange capacity, thus giving a value which should be roughly proportional to the availability of the cations to the plant. The trends in nutrient level, expressed in these terms, correlate very well with soil pH and with the limits of certain species, independently of soil type. These results are discussed more fully on page 37. The work will be extended to other flushed sites because these provide ideal environmental gradients for such studies.

In addition investigations have been started on the variation of soil moisture and the rate of diffusion of oxygen. Soil moisture is being determined by the gypsum resistance block technique and rate of oxygen diffusion by a platinum electrode method. The required apparatus has been constructed and, since preliminary results have been promising, extensive field experiments are planned.

From the same cores, which provided soil for chemical analysis, over nine hundred tillers of the following species were isolated:—*Festuca rubra, F. ovina, Agrostis tenuis, A. stolonifera, Poa annua, P. pratensis, P. subcaerulea, Holcus mollis* and *Anthoxanthum odoratum*. These isolates were cloned, grown in a replicated trial and some preliminary information has been obtained from the observations and measurements obtained. The initial problem of determining which isolates represent different genotypes is a major one and tentative groupings require further study.

The first of a series of schemes for experimenting with artificial flushing has been initiated in the Pentland Hills. Spring water is being conveyed about 160 feet and allowed to run on to an area in which *Nardus stricta*, *Festuca ovina* and *Deschampsia flexuosa* are prominent on a moderately steep slope. Using a half-inch polythene pipe under these conditions it has been calculated that up to 120 gallons per day can be supplied. Probably it will be possible to make technical improvements chiefly connected with the mode of intake of water and the prevention of blockage by silt which will give an improved rate of flow. Prior to the start of irrigation, samples of soil and plants were taken from the area both for analyses and for the purposes of a record, and further samples will be taken at intervals.

It is a matter of common observation that where intra-specific populations are found growing in two or more distinctive habitats such habitat populations often exhibit well-marked phenotypic differences, e.g., differences in plant size, habit of growth, time of flowering, &c. In cross-pollinated species occurring in different habitats which are not spatially isolated it is difficult to see how these phenoecodemes can reflect more than varying degrees of character plasticity, yet even in wind-pollinated species such as *Agrostis tenuis*, *A. canina*, *Festuca ovina* and *Plantago lanceolata* some evidence has already been obtained which shows that the lack of spatial and temporal isolation does not preclude the possibility that habitat populations are also genoecodemes.

There is, however, a strong tendency for the two species of *Agrostis* as well as the two cytodemes of *Festuca ovina* to be ecologically separated and for *Plantago lanceolata* to be confined to the more fertile areas and this uneven representation in the range of habitats imposes a serious handicap upon the usefulness of these species when the goal is to obtain an understanding of the interplay between plant and varying environments. Therefore, it was a species which might well be considered to be of little agricultural value, namely *Potentilla erecta*, which has, in fact, proved to be potentially the most interesting simply because of its abundant occurrence throughout a wide variety of plant communities. A garden trial which contained representative samples of one hundred and sixty-five *P. erecta* populations collected from sites typifying a number of phytosocial environments has yielded data which strongly suggests that genoecodemes can be recognised with comparative ease and certainty in this species. In all the quantitative characters measured, with the exception of flower and petal size, there were very highly significant differences particularly between values for populations originating from closely grazed bent fescue habitats and those from *Molinia*-dominated communities; further it so happened that at fourteen sites within the area of sampling these two habitats were scarcely spatially separated, and when these fourteen pairs alone were analysed the same high order of inter-population significance was obtained in the following characters: Plant Diameter in two years, Length of the First (longest) Internode, Leaf Length, a slightly reduced significance in Number of Leaf Teeth but no significant difference at all in Time of Flowering. Reducing the number of community pairs to the ten which were truly contiguous, even with the smaller number of degrees of freedom, Plant Diameter, Length of the First Internode and Leaf Length still gave very highly significantly different values, and again, Time of Flowering values were completely non-significant. Such a high degree of differentiation between contiguous pairs of populations from contrasting environments scattered throughout a considerable area, and including one pair from the North of Scotland, cannot be dismissed as fortuitous and is undoubtedly worthy of further investigation. In the hope of obtaining further information on this subject, three pairs of populations from contiguous and contrasting habitats which had been sampled previously together with a fourth pair from the North of Scotland were sampled more intensively and systematically than before and this time collections of seed were also made wherever possible. In addition to measuring the length of the flowering stem and the length of the first internode on the plants as collected, floristic lists were compiled and soil pH and mineral analyses were later carried out. Analyses of variance calculations on stem and internode data gave evidence of marked phenoecodemes in the two phytosocial environments of bent fescue and *Molinia*-dominated vegetation at each site.

The search for outstanding genotypes from ecotypic populations which could be used as parental material to build up stocks of improved seed of some of the native grasses has been borne in mind. Such seed might be of first importance for sowing on hill areas treated by irrigation. A number of seed lots of *Agrostis tenuis* crosses are currently being grown and will be included in further trials.

The work of development of small plot techniques for the assessment of yielding ability of Italian ryegrass progenies was continued. In a trial using fourteen "simulated progenies" (seven varieties and seven mixtures of two varieties in equal proportion), three small plot treatments were compared with broadcast swards in a split plot layout. The three treatments were: one yard square plots with three-inch spacing between plants; one yard square seeded plots with the plants in rows three inches apart; and two yard square plots with the six-inch spacing between plants. The trial was cut four times during 1962 and dry-matter yields recorded. No significant variety x plot types interactions were present except in the third harvest where the interaction was significant at 5 per cent and was largely due to the behaviour of the plots at six-inch spacing. The yields per unit area were approximately constant under any of the densities studied—*i.e.*, the relationship between relative log yield per plant and log density was effectively linear. The highest yields (total over four cuts) were recorded in the 3" × 3" spacing (12,000 lbs. DM/acre) and the lowest in the 3" rows (10,800 DM/acre). The highest yielding variety (average over all spacings) was Melle (11,800 lbs./acre) and the lowest S22 (10,500 lbs./acre).

It is possible that any of the three plot types in the trial would be suitable for progeny testing during the early stage of a breeding programme—probably the most useful being that with the plants at 3" spacing. The sown rows gave slightly more satisfactory results (*i.e.*, more nearly in accord with the results from the sward plots) but require larger quantities of seed. It is worth noting that the 3" and 6" spacings permit indentification of individual plants and might be useful for single plant selection purposes.

An investigation into the relationships between the components of yield and more particularly the components of rate of leaf area increase in young seedlings of Italian ryegrass has been started with the intention of assessing the heritability of these components. The yielding ability of progenies from parents selected for high rate of leaf area increase could then be examined using one of the small plot techniques described above. Individual plants will be selected on the basis of uniformity of time of flowering and used to produce polycross progeny in 1964.

Oats.—The technique of inoculating oat seedlings with a suspension of oat stem eelworm has provided an efficient and satisfactory method of selecting resistant plants from segregating hybrid material.

Avena ludoviciana and some hybrid lines derived from it are outstanding and possess a degree of resistance superior to that found in any of the other material tested. As already mentioned in a previous Report *A. ludoviciana* is believed to combine two types of resistance ; one type depending on a " tolerant " reaction enabling the plant to support a number of eelworm in its tissues without growth being seriously retarded, and the second an " inhibitant " reaction where eelworm multiplication in the plant is restricted. Plants which approximated to the *A. ludoviciana* degree of resistance, and which were superior to either parent, as well as plants which were more susceptible than either, were obtained from a cross between the cultivars Early Miller (tolerant) and Milford (inhibitant).

Resistance of the Milford type is reported to be due to a single dominant gene. This has been confirmed in field-grown material and at low dosages when the effect measured is the degree of dilation of the plant base. However, with the high dosage of the inoculation tests, 300 eelworm per seedling, the heterozygotes exhibit dilation with the result that plants homozygous for the inhibitant gene become readily recognisable.

The effect of the gene for tolerance is reflected in plant height. Although plant height may also be affected by such factors as variations in dose and in the vigour of the individual seedlings at the time of inoculation, in plants which are free from dilation the tallest plants represent the homozygous tolerant gene.

Following inoculation tests in the F_2 and F_3 generations 235 lines resulting from *A. ludoviciana* (resistant) × ' Blenda ' (susceptible) each stemming from a different F_2 plant were allocated to the nine theoretical genotypes obtained from a diploid segration of two independent genes. Of these 212 were classified according to their phenotypes in the F_3 test, and the remaining 23 according to the appearance of the plants in the F_2 test wherein they were either killed or barren.

Avena ludoviciana (resistant) × ' Blenda ' (susceptible) : classification of an F_2 in nine theoretical classes

Class	*Genotype*	*Description of Symptoms and Phenotype*
1	Hom. Tol. Hom. Inh.	Tall plants, no dilation, *A. ludoviciana* type.
2	Het. Tol. ,, ,,	Segregating for height, no dilation.
3	Hom. Intol. ,, ,,	Plants, stunted, no dilation, Milford type.
4	Hom. Tol. Het. Inh.	Height variation attributed to segregating dilation.
5	Het. Tol. ,, ,,	Segregating for both height and dilation.
6	Hom. Intol. ,, ,,	All plants below normal height, height variation attributed to segregating dilation.
7	Hom. Tol. Hom. Uninh.	All plants above average height, all dilated, Early Miller type.
8	Het. Tol. ,, ,,	Segregating for height, all dilated.
9	Hom. Intol. ,, ,,	All plants stunted, all dilated, susceptible, Blenda type.

Hom. = Homozygous. Tol. = Tolerant. Inh. = Inhibitant.
Het. = Heterozygous. Intol. = Intolerant. Uninh. = Uninhibitant.

	$F_3 + (F_2)$	*Group Totals*	*Predicted*	*Group Totals*	*Predicted fraction of total*
1	14	14	15	15	1/16
2	13	160	29	161	2/16
3	2 + (3)		15		1/16
4	28		29		2/16
5	80		59		4/16
6	25 + (9)		29		2/16
7	10 + (2)	61	15	59	1/16
8	32		29		2/16
9	8 + (9)		15		1/16
	212 + (23)	235		235	

Fourteen lines were classed as homozygous for both genes for resistance, and 17 for the absence of both, figures which are very close to the predicted figure of 15 assuming a 15 : 1 ratio—again 54 were classed as Tolerant and 56 as Intolerant compared with the predicted figure of 59 in a 1 : 2 : 1 ratio, which ratio also applies to the 61 lines classed as Uninhibitant.

All this is suggestive of the major gene effect of two independent factors for resistance, but in the material under test, differences in degree of susceptibility or resistance between varieties, and between hybrids in which different susceptible varieties have been used as parents point to the existence of modifying genes, as also do differences in degree between lines of the same apparent genotype within a hybrid.

Good argonomic types selected from second and third backcross hybrids between high yielding parents and the eelworm resistant *A. ludoviciana* were again included in replicated trials at Pentlandfield in 1962 on eelworm free land, while check plots on infested soil were grown to confirm their resistance to natural attack. A number of these types showed considerable promise and some, which, in addition to a good yield of grain, gave high yields of long resilient straw, are being incorporated in the yield trials at the Argyll and Inverness-shire selection centres where it is thought that such straw may be a valuable attribute. Grain yields approximating to those of Blenda are now being obtained and of the 256 resistant lines in preliminary trials 1962, 59 have given yields of at least 90 per cent of Blenda, while a number of them have exceeded it.

A new selection centre in Inverness-shire in the same climatic environment as the old, but on a better class of land, was established in 1962 near Dulnain Bridge. At the same time facilities at Daviot for continued trial of the many selections already made on the lighter land have been retained. Experience has shown that while selection in the Inverness-shire environment has in the past tended to provide straw-producing types, there was little tendency to lodge on the light land. With quality and quantity of straw assuming a greater importance as a result of the general decline in oat cultivation in Scotland it was felt that selection for strength of straw in the early generations at this selection centre would be more efficient on a better class of land.

During the year a plot, infested with Cereal Root eelworm (*Heterodera Avenae*), has been established at Pentlandfield as a preliminary to the study of resistance to this pest. In the first instance resistance in Oats will be the main consideration but some attention will also be paid to Barley, the cultivation of which is on the increase in Scotland.

For the past three years, thanks to facilities granted by the

Forestry Commission, trials have been carried out at a centre on sandy soil with a high pH value in East Lothian. The trials have been conducted to select oats suitable for areas where manganese deficiency in the soil causes grey speck disease and where drought conditions are a problem. So far, hybrid lines from *Avena ludoviciana*, originally selected for resistance to stem eelworm, and lines from hybrids of the black oat variety Rothenburger show considerable promise. Stocks of these are being built up for trial in similar conditions in other parts of the country.

Barley.—Following representation from Scottish Brewers and Maltsters to the Department of Agriculture and Fisheries for Scotland a co-operative programme with the Plant Breeding Institute, Cambridge, was instituted in 1962. As a preliminary study 52 F_4 and F_5 generation lines of hybrid HB.380 were sown in replicated plots at Pentlandfield together with a representative selection of barley varieties. The material was assessed on Field characters during the growing season, and after harvest the produce was returned to Cambridge for a further assessment of grain characters and malting quality.

Potatoes.—A seedling selection, Reference No. 2403a(1), bred from Roslin Riviera × Dr McIntosh, has successfully completed the Merit Trials conducted by the Department of Agriculture and Fisheries for Scotland and has received "Commendation." It has been named 'Pentland Falcon'.

The Registration Authority's Official description of 'Pentland Falcon' is as follows :—

Maturity .	Early Maincrop.
Tuber . .	Oval to kidney (long oval), slightly flat, tapering at heel end ; skin white ; flesh white, fairly crisp ; eyes shallow, mainly on the shoulder ; sprouts blue.
Foliage Type	Majestic.
Foliage .	Haulm of medium height, erect, fairly bushy, later spreading ; stems average in number, fairly thick, branching, mottled purple ; cover good ; leaf of medium size, fairly broad, open ; leaflets medium green, oval fairly thick ; petiole fairly long ; secondary leaflets moderate to frequent, small, rounded, occasional petiolar leaflets.

Flower .	White, faint purple on backs of petals, frequent, fairly small ; anthers orange, slightly irregular ; inflorescence stalks mainly green, cork-ring dark red ; buds green, oval ; sepals mainly irregular, green, dark at base ; berries occur.
Remarks .	Cropping : very good ; cooking quality very good ; keeping quality fairly good ; field-immune from viruses A and B, foliage resistant to the common strain of blight ; fairly resistant to dry rot ; susceptible to gangrene ; moderately susceptible to skin spot.

A red-tubered variant of Pentland Beauty has completed the Wart Disease and Identity Test and has been registered under the name 'Red Pentland Beauty'. Four selections raised at the Plant Breeding Station and grown commercially in East Africa under the names Roslin Eburu, Roslin Mt. Kenya, Roslin Elmenteita and Roslin Chania were entered for the final year of the Wart Disease and Identity Test (1963) with a view to having these names registered.

The Merit trials conducted by the Department of Agriculture and Fisheries for Scotland in 1963 contain thirty seedling selections raised at the Plant Breeding Station. Of these, eighteen are in the 1st Year, seven in the 2nd Year and five in the 3rd Year of trial. Initial tests have shown that twelve of the thirty seedlings are resistant to blight caused by race 1, 2, 3, 4 of *Phytophthora infestans* (Mont.) De Bary and that eight are resistant to Common Scab. Resistance to the potato root eelworm is present in four selections. Ten of the entries gave a necrotic reaction to virus Y and may, therefore, be regarded as resistant while fifteen proved to be hypersensitive to virus X.

Samples of 616 selections were forwarded to the Department of Agriculture and Fisheries for Scotland for inclusion in the Wart Disease (single tuber) tests.

The trial and multiplication plots at the Station's isolation centre at Blythbank in 1962 covered approximately 8 acres. They consisted of 11,700 single tuber plots, 1,930 3-tuber plots, 384 8-tuber plots and 150 40-tuber plots together with plots of the Merit Trial seedlings, the largest of which covered half an acre. The multiplication plots of all the seedlings entered for the official tests in 1962 were examined for virus content. Fully 2,000 leaf samples were taken during the growing season and tested serologically for the presence of viruses X and S. No infections were detected and no virus Y symptoms were observed in any of the plots. A few leaf-roll affected plants were, however, found late in the season.

All the seedlings entered for Merit Trials were tested under greenhouse conditions for their reactions to infection with viruses A, B, C, X and Y. In addition greenhouse tests for reactions to infection with viruses X and Y were carried out on about 350 seedlings in the early stages of multiplication.

Breeding for blight resistance has been continued with the object of producing new commercially acceptable types possessing firstly, a high degree of field resistance to the disease, and, secondly, as many R genes as possible. In recent years race 1, 2, 3, 4 of *P. infestans* has been employed for screening purposes since reactions to this race indicate a measure of field resistance in plants possessing any or all of the four known R genes and determine the presence of new R genes by inducing a hypersensitive reaction. The field resistance of a number of breeding lines possessing new R genes has been determined by exposing samples to infection under field conditions in Mexico through the generous co-operation of Dr J. S. Neiderhauser of the Rockefeller Foundation. Four of the selections showing resistance to blight under Mexican conditions have been entered for the Merit Trials of the Department of Agriculture and Fisheries for Scotland. In 1962 samples of ninety-five seedlings bred for resistance to blight were forwarded to Mexico for test under natural conditions in the field. The results showed that twenty-five of them had effective resistance in that environment.

New resistance genes have been detected in seedlings derived from *Solanum demissum*, *S. stoloniferum*, *S. vernei* and *S. x edinense*. The latter is a naturally occurring hybrid between *S. demissum* and *S. tuberosum* subsp. *andigena* found in Central Mexico. Differences between these new R genes have come to light in the course of tests but it is not yet known exactly how they are related. The purpose of accumulating R genes in a background of field resistance is to build up hypersensitivity to the more common races of the disease and to hold in check by means of field resistance any new races that might arise.

In the more advanced breeding work the main sources of field resistance have been Roslin Eburu, bred originally from

S. demissum and *S. phureja*, seedling 1705(5) derived from *S. simplicifolium*, *S. phureja*, and *S. demissum* and several selections of Mexican origin supplied by Dr J. S. Neiderhauser. No new R genes are present in these parental types and the level of field resistance ranges between Group 2 and Group 3 on the arbitrary scale 1-5 where Group 1 represents complete resistance and Group 5 extreme susceptibility. Field resistance in the progenies can readily be ascertained by screening with race 1, 2, 3, 4.

During the past year fully 2,500 seedlings, representing thirty-six sample progenies, were raised and screened in order to study the inheritance of resistance and to determine which crosses should be raised on a larger scale for routine selection. The resistant survivors of these pilot tests were grown to maturity and retained for selection under field conditions in 1963. The resistance of about 200 advanced selections was determined by growing plants in pots and inoculating them under laboratory conditions with race 1, 2, 3, 4.

A collection of wild species of *Solanum* and a number of hybrid seedlings was examined by inoculating detached leaves under controlled conditions, and assessing resistance on the basis of lesion size and extent of sporulation. Some of them were found to be completely resistant to infection.

Further investigation was made of the nature of "field resistance", particularly the apparent loss of virulence of *P. infestans* as a result of its being transferred from leaf to leaf of the same variety. Detached leaves and race 1, 2, 3, 4 of *P. infestans* were used. The lesions which developed after four passages through the leaves of twenty-two cultivars were smaller than those which developed on leaves of the controls which were inoculated with spores from leaves of $R_1R_2R_3R_4$ differential host. Sporulation decreased continuously during three passages through the leaves of eighteen of the cultivars and in eight it continued to decrease after a further transfer. In the remaining ten, sporulation increased following the final transfer but, with one exception, it was less than that resulting from the primary inoculation.

In continuing the investigations on resistance to common scab, 500 seedlings which showed little or no scab in 1961 were grown again in the greenhouse and re-assessed for degree of resistance. The more promising economic types were selected for further trial in the field in 1963.

Progenies of fourteen crosses were raised in the greenhouse in soil inoculated with *Streptomyces scabies* Waksm. and Henrici, and their susceptibility to scab was assessed. In order to compare results obtained in the greenhouse and in the field all clones in six progenies were retained for further tests in the thoroughly infected field plots at Archerfield, East Lothian. Selections from the remaining progenies were kept for trial as economic types. Last season 236 cultivars and advanced seedlings were grown at Archerfield. The susceptible varieties used as controls were severely affected by scab while varieties reputed to be scab resistant were less severely affected. A number of the advanced seedlings developed less scab than such resistant varieties as Ackersegen, Cherokee, Frühperle, Ontario, Panther and Seneca. Of these seedlings, fourteen had a lower cover score and twenty-one a lower damage score than Frühperle which was the most resistant of the named varieties.

The investigation of genetic differences between strains of potato root eelworm was continued on the basis that biotypes of strain 1 have a normal chance of encysting in potatoes incorporating the gene H_1 ex *S. tuberosum* subsp. *andigena* and a negligible chance of encysting in potatoes incorporating the gene H_2 ex *S. multidissectum*, biotypes of strain 2 *vice versa*. These dominant genes act independently and it was stated in last year's Record that a so-called F_1 eelworm population, produced by multiplying an equal mixture of strains 1 and 2 on recessive potatoes having no resistance to either strain, included no recombinant biotypes capable of encysting in potatoes of genotype H_1H_2.

In 1962, an F_2 population, produced by multiplying the original F_1 population on recessive potatoes and an F_1 population of the same age were both adjusted to 40 and 80 eggs/gm. infectivity in sand; this and the unmixed populations of strains 1 and 2 at 40 eggs/gm. infectivity made six culture media in which 18 clones of genotype H_1H_2 were grown, one plant of each clone in each culture medium. Recessive potatoes were grown in each culture medium as susceptible controls.

Practically no cysts appeared on the potatoes of genotype H_1H_2, confirming the previous year's results with the F_1 population and indicating that recombinant biotypes had failed to segregate out in the F_2 population. The percentages of eggs which developed into cysts in the recessive potatoes infested by the unmixed populations were more than twice the corresponding percentages in the F_1 and F_2 populations, so that there was at least a possibility, worthy of further investigation, that crossbred biotypes as a class were weak or nonviable and incapable of encysting even in recessive potatoes.

In the course of the breeding work it was found that the apparently comprehensive resistance of *S. sanctae-rosae* (P.H. 328) comprised specific resistance to strain 1 in combination with specific resistance to strain 2. The dominant gene conferring the resistance to strain 1 was indistinguishable in effect from the H_2 gene of *S. multidissectum*. Another dominant gene was probably responsible for the resistance to strain 2, but conferred a lesser degree of resistance than the H_1 gene of subsp. *andigena*.

There was some evidence of dissociation of resistance to strains 1 and 2 in the breeding line stemming from *S. vernei*, despite the fact that the resistance in this case is polygenic. In unreplicated tests of resistance on F_2 material raised from crosses between selected hybrids (*S. vernei* × *S. tuberosum*) some seedlings appeared to be more resistant to strain 1 than strain 2, others *vice versa*. This will be followed up by replicated tests of resistance.

Following an exchange of material with Prof. H. Ross of the Max Planck Institute, Cologne, and Dr C. A. Huijsman of the Netherlands Plant Breeding Institute, Wageningen, it appeared that strains 1 and 2 at Pentlandfield could be differentiated almost equally well by means of potatoes incorporating dominant genes ex subsp. *andigena*, *S. kurtzianum* and *S. famatinae*, in which cases strain 1 was the resistance-breaking strain, and *S. multidissectum* and *S. sanctae-rosae*, in which cases strain 2 was the resistance-breaking strain. Ross and Huijsman each had A and B populations which could be differentiated roughly along the same lines, corresponding to strains 2 and 1, respectively, at Pentlandfield.

Summing up, it may be too pessimistic to suppose that the whole range of resistance-breaking biotypes arises regularly by mutation in every eelworm population. It is quite possible that certain kinds of resistance-breaking are characteristic of naturally occurring races which have diverged genetically to the extent that recombination of resistance-breaking factors occurs rarely or not at all when they mingle in the same field.

There seems to be no foreseeable prospect of breeding potatoes with comprehensive and lasting resistance to potato root eelworm. The actual objective is much more limited, based on the fact that a variety incorporating strain-specific resistance can probably be grown for several years in succession in an infested field before the emergence of a resistance-breaking strain can be detected. With a normal rotation of crops, this means that ten to twenty years could elapse before the population in such a field would begin to increase again, having declined to a very low level in the meantime. It is to be hoped that a variety resistant to the emergent strain would then be available to continue the process of control.

Breeding for the combination of resistances to different viruses was continued and over 7,000 seedlings were inoculated with virus X and/or virus Y in the glasshouse. Subsequently, about 4,800 seedlings were planted in the field for selection on the basis of economic characters. After further tests in the glasshouse during the winter, about 400 seedlings have been selected for extended trial. Earlier selections were included in trials at Elvingston, East Lothian, and at Cambridge in 1961. The results of these trials were evaluated at Pentlandfield in 1962. At Elvingston, there was an overall spread of leaf-roll to 51 per cent of the plants in the main trials with little interference, only 6 per cent infections, from virus Y. Pentland Crown with 20 per cent infection again showed reasonable resistance to leaf-roll and an outstanding result was obtained with seedling G2076(28) which contracted only 4 per cent infection. This seedling and 72 others were selected for further trial and for inclusion in the leaf-roll resistance breeding programme. At Cambridge, leaf-roll infections were observed in 47·5 per cent and infections with virus Y in 44·8 per cent of the plants in the main trials. One advanced seedling 2601d(22) showed no infection with virus Y and 16 seedlings were selected for combined resistance to leaf-roll and virus Y.

The material from Elvingston and Cambridge was used experimentallly to assess the value of leaf-roll detection in the tuber by a resorcinol-blue test which reveals callose plugs developed as a result of leaf-roll infection. Agreement between the test and field observations was reached in 90·2 per cent of cases in the examination of 1,778 tubers. Agreement was particularly good in the tests of material in the main trials which consisted of 50 plants of each clone entered and the variations recorded between clones by the tuber test were similar to those observed later in the field. If this level of agreement is maintained in further trials it should be possible to rely on the tuber tests alone and dispense with the evaluation plots in the field. Tests completed on tubers from the 1962 trials at both centres have indicated that the spread of leaf-roll was not as extensive as in 1961. A further point of interest arising from the tests on tubers is the detection of callose plugs in certain seedling material hitherto considered to be highly resistant to leaf-roll. It would seem that this material may be infected with the virus although it shows no clear symptoms in the haulms under Scottish conditions. This possibility is receiving attention.

The results of experiments on the reaction of Dische diphenylamine reagent with sap from potato plants infected with leaf-roll virus have been published (see summary p. 24).

Investigations into the relationships of genes controlling reactions and resistance to X and Y viruses are being continued with diploid, tetraploid and hexaploid species as experimental material. Within the diploid series evidence was obtained of linkage between a gene controlling resistance to virus X and a gene controlling resistance to virus Y in *S. chacoense* and also between a gene controlling resistance to virus X in *S. sparsipilum* and a gene controlling resistance to virus Y in *S. chacoense*. In both cases, however, disturbed segregations obscured the detailed picture of gene relationship.

In tetraploids, a gene with the combined properties of Nx and Nb has come to light in *S. tuberosum* subsp. *andigena*. A similar gene was found previously in *S. acaule* and breeding procedures to examine the relationships of the two were begun. From analysis of progenies of *S. stoloniferum* it now seems possible that there may be six or seven genes concerned in determining the reactions of this species to the virus Y complex. Experiments to clarify this situation and to determine the gene relationships are in progress. The collection of haploids derived from tetraploid *S. tuberosum* subsp. *tuberosa* and *andigena* were examined for reactions to two strains of virus X and three strains of virus Y. Several clones of potential genetic value were detected but difficulties were encountered in breeding and no useful seed was obtained.

Breeding difficulties and the occurrence of high proportions of nonviable and abnormal seedlings in the progenies of hybrids between *S. spectabile* and *S. demissum* have interfered considerably with progress in the investigation of hexaploid material. Nevertheless, from the small number of normal plants raised, evidence was obtained that the gene controlling high level resistance to virus Y in one line of *S. spectabile* is independent of the allelic pair of genes controlling necrotic responses to virus Y in *S. demissum*.

In an extension of the investigation into the genetics of immunity from virus X, seven immune seedlings were obtained from 819 seedlings raised from 17 inter-crosses between selected susceptible parents. This number is quite inadequate to support the view that the immune seedlings are the results of recombination of complementary genes controlling immunity but the possibility of the seedlings possessing recessive genes for immunity, a possibility previously suggested, is real and will be investigated further.

Studies have been started to elucidate the genetic control of immunity from virus S in potato.

An unusual strain of virus X brought to our notice by Dr R. K. McKee, John Innes Institute, has been studied in its effects on a range of potato varieties and species of varied genetic types. There appears to be no doubt that this strain falls into Group 4 of our classification and as such is the first representative of this Group to be encountered. A note on this virus will be found on page 26.

By aphis transmission from plants jointly inoculated with potato viruses Y and C, Dr Marion Watson of Rothamsted Experimental Station obtained mixed isolates having some of the properties of both viruses. Dr Watson thought it likely that the isolates contained particles carrying genetic determinants from both viruses. In an attempt to obtain more positive evidence for or against this interpretation, a number of potato varieties and seedlings, known to be necrotic in varying degrees to virus Y, were inoculated with potato virus C, a number of potato virus Y strains and their mixtures with virus C. This attempt to select a potato genotype which could be used to isolate virus particles carrying a Y-type determinant from those carrying a C-type determinant was unsuccessful; all genotypes that were hypersensitive to virus Y were either hypersensitive to virus C or developed a lethal systemic necrosis.

In further studies on possible genetic recombination of viruses, attempts were made to isolate a Group 4 strain of virus X from mixtures of strains from Group 2 and Group 3 respectively. These attempts were unsuccessful and alternative approaches to the problem will be sought.

The tuber-bearing *Solanum* species in the Birmingham University Collection have been examined for virus content and reactions to viruses X, Y and S. This work is now complete and the results are reported in the Occasional Paper on page 30.

Publications

GOVIER, D. A. (1963). The reaction of the Dische diphenylamine reagent with sap from potato plants infected with potato leaf-roll virus. *Virology*, **19.**

Brandenburg (Phytopathol. Z. **43,** 420-424) reported the mechanical transmission of potato leaf-roll virus in phenol extracts of infected potato plants when the extracts had been incubated with ribonuclease. He also reported that, whereas ribonuclease treatment appeared to be necessary for successful transmission, incubation with deoxyribonuclease reduced the frequency of infections; from these results he concluded that potato leaf-roll virus was present in the plant as free deoxyribonucleic acid (DNA). Actuated by this conclusion, Brandenburg applied the Dische diphenylamine test, a well-known test for DNA, to expressed saps and found that saps from potato plants infected with leaf-roll virus gave a blue colour whereas saps from healthy potato plants gave a pale-green colour. Attempts were made to confirm Brandenburg's results and conclusions with the following results:—

Potato leaf-roll virus was not transmitted mechanically in phenol extracts with or without ribonuclease treatment.

Sap from potato plants infected with leaf-roll virus gave a blue colour when treated with Dische diphenylamine reagent. The colour was shown to be produced by fructose and sucrose, which were found in much higher concentration in sap from these plants than in sap from healthy plants.

Gregor, J. W. (1962). Genecological (biosytematic) classification: the case for special categories. *Regnum Vegetabile*, **27.**

Attempts to assimilate genecological information into orthodox taxonomy either by adding categories based on criteria other than morphological, or by redefining the orthodox categories on the basis of other criteria are virtually an admission that much genecological information is not amenable to taxonomic treatment along traditional lines.

How to systematise genecological findings has been the subject of much discussion, and classifications based on the criterion of ability to exchange genes have been proposed, *e.g.* the coenospecies-ecospecies-ecotype hierarchy. But gene exchange capacity is only one of a number of situations of interest from an evolutionary point of view, and consequently in defining genecological entities different situations will occasion the use of different criteria. Clearly no classification involving an hierarchy of mutually exclusive categories can, in those circumstances, be generally applicable. In order to facilitate the communication of genecological information and ideas what seems to be needed most is a logical series of generally acceptable terms covering elements associated with the more important genecological situations, *e.g.* association with habitat, association with locality, reproductive behaviour, gene exchange capacity and so on. The deme terminology aims at providing such a series. A feature of this terminology is the construction of category terms by the addition of one or more virtually self-explanatory prefixes to a neutral suffix—*deme*.

This suffix denotes any group of individuals of a specified taxon: prefixes distinguish the genecological situations. While no deme category is directly related to any category of orthodox taxonomy, any group of individuals assigned to a deme is, nevertheless, referable to a named taxon. Thus, despite their separate terminologies and different purposes, orthodox taxonomy and the deme system of recording micro-evolutionary elements which by their very nature are not amenable to orthodox treatment, are in no respects antagonistic, but, on the contrary, are truly complementary.

NOTE ON AN UNUSUAL STRAIN OF POTATO VIRUS X

G. Cockerham and T. M. W. Davidson

Strains of potato virus X have been classified into four groups on the basis of their relationships with the genes Nb and Nx which, in cultivated varieties of the potato, determine hypersensitive responses to infection and hence field immunity from the causal virus (Cockerham, 1943, 1954). There are many examples of strains which activate both Nb and Nx, strains which activate Nb but not Nx, and strains which activate Nx but not Nb and thus fall into Groups 1, 2 and 3, respectively, of the classification adopted (Cockerham, 1954, Köhler, 1962). The postulated Group 4 would contain strains which activate neither Nb nor Nx but hitherto the only evidence of the existence of such a strain was found in a reference to the strain X^a (Bawden and Sheffield, 1944) which was reported to cause a non-lethal mottle disease in the varieties Epicure and King Edward, each of which possesses Nx, and to be carried without symptom expression in the varieties Arran Victory and President, each of which possesses Nb. The strain X^a has never been available for full study, however, and no other strain with the requirements essential to classification in Group 4 has been encountered though many attempts in several forms of experimental approach have been made to secure such a strain. It was with great interest, therefore, that we learned from Dr R. K. McKee, John Innes Institute, that he had found in the variety Pentland Beauty, which possesses both Nb and Nx, a virus which reacted positively with anti-X serum. This virus has apparently reached the Pentland Beauty through a graft transfer from an Ecuadorian clone of *Solanum tuberosum* subsp. *andigena*, C.P.C. 2971. For the purpose of further examination, Dr McKee very kindly provided tubers of C.P.C. 2971 and of the infected Pentland Beauty and this note records the results of a short series of tests carried out on this material since its receipt.

Plants raised from C.P.C. 2971 and the infected Pentland Beauty were all conspicuously affected by mosaic disease, and sap from each gave a strong agglutination reaction when tested with our anti-X serum. This suggested that virus X was present in each source and consequently attempts were made to confirm this indication and to determine the strain type or types concerned. For this purpose a selection of potato varieties and clones of known genetic constitution were chosen as test plants and each was inoculated on three leaves, previously dusted with carborundum powder, with undiluted sap taken from one or other of the two sources, C.P.C. 2971 and Pentland Beauty. There were thus two series of test plants, one for each source, and two plants of each variety or clone were inoculated in each series.

Inoculation from C.P.C. 2971 gave the following results. The varieties Majestic and Up-to-Date, both lacking Nb and Nx, showed strong mosaic symptoms and their saps reacted positively with anti-X serum. The varieties Arran Victory and Craigs Alliance, both possessing Nb but not Nx, showed local lesions on the inoculated leaves but there was no systemic invasion and serological tests were negative. The varieties Arran Pilot and President, also possessing Nb but not Nx, showed neither local nor systemic symptoms and serological tests were negative. Arran Crest and King Edward, both possessing Nx but not Nb, responded to inoculation by showing severe mosaic symptoms whereas Craigs Royal, of the same genetic type, showed no symptoms. In all three cases serological tests were positive and confirmed the presence of an X virus. The variety Craigs Defiance which possesses both Nb and Nx was entirely unaffected by the inoculum. The clone C.P.C. 2113-1 is of the species *S. acaule* and it possesses a gene which has the properties of a combination of the genes Nb and Nx and consequently responds to all strains of virus X in necrotic fashion. In the present case, inoculation from C.P.C. 2971 caused local lesions but no systemic penetration of the virus as indicated by negative serological tests. The variety Saco and U.S. seedling 41956 are immune from virus X as also are the *S. acaule* clones R/50/13 and C.P.C. 379.1. None of these plants became infected by inoculation with sap from C.P.C. 2971.

The above reactions show that the source C.P.C. 2971 contained a virus which was fully resisted by plants immune from virus X, which caused local lesions only or no symptoms in the presence of the necrosis-inducing gene of *S. acaule* and the gene Nb, and which invaded systemically varieties possessing the gene Nx only or neither of the genes Nb and Nx. It seems clear, therefore, that the virus, which reacts with anti-X serum, is a strain of virus X assignable to Group 2 of the classification.

Inoculations made from the Pentland Beauty source gave similar results to those already described for the C.P.C. 2971 source in causing no response and no recovery of virus from the X-immune clones Saco, 41956, R/50/13 and C.P.C. 379.1; local lesions but no recovery of virus from C.P.C. 2113.1; severe mosaic responses with recovery of virus X from Arran Crest and King Edward; and no symptoms with recovery of virus X from Craigs Royal. The results differed, however, on varieties possessing the gene Nb. Thus the virus from Pentland Beauty caused a mosaic disease on Arran Pilot and a severe mosaic with necrotic flecks on Arran Victory, Craigs Alliance and Craigs Defiance. Sap expressed from each of these varieties reacted strongly with anti-X serum.

These results confirm the virus as virus X and indicate that it fulfils the requirements for classification as a Group 4 strain. It is interesting to note that although the strain infects systemically varieties of the phenotypes nb : nx, Nb : nx, nb : Nx, and Nb : Nx with the production of varying symptoms, it causes local lesions only in the presence of the necrosis-inducing gene in *S. acaule* and it is fully resisted by the X-immune types of both *S. tuberosum* and *S. acaule*.

The symptoms caused by the two strains on tobacco and on those potato varieties which both infect systemically are rather striking and very similar and evidence is accumulating to suggest that the similarity extends to other characteristics, namely, serological and physical properties. In these circumstances it seems possible that the two strains are closely related and that the Group 4 strain may have been derived from the Group 2 strain by a simple mutation against the action of the Nb gene. It is odd, therefore, that no recovery of the Group 4 strain was made directly from C.P.C. 2971. This problem together with other aspects of relationship are the subjects of further enquiry now in progress.

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REPORT ON THE VIRUS CONTENT AND THE REACTIONS TO VIRUSES X, S AND Y OF TUBER-BEARING SOLANUMS COLLECTED BY THE BIRMINGHAM UNIVERSITY EXPEDITION TO MEXICO AND CENTRAL AMERICA, 1958.

G. Cockerham, T. M. W. Davidson
and A. W. Macarthur

This report is confined to tuber-bearing *Solanum* material received as tubers from Professor J. G. Hawkes, leader of the Birmingham University Plant Collecting Expedition to Mexico and Central America, July-December 1958. Six parcels of tubers were received direct from Central America between August 1958 and March 1959 and one parcel of tubers consisting of material which had been grown once in Birmingham was received in March 1960. Some tubers were rotten on receipt and others rotted in pots after planting. For these reasons, no tests were possible on lines of *S. bulbocastanum* 1922; *S. brachistotrichum*, 1284; *S. agrimonifolium* 1889; *S. fendleri*, 1177 and 1217; *S. stoloniferum*, 1298. Many tubers germinated and produced plants but no tubers and such lines were examinable for virus content but not for reaction to viruses. They include *S. morelliforme*, 1809; all lines of *S. clarum*, 1776, 1777, 1778, 1813, 1824, 1827 and 1894; *S. brachistotrichum*, 1313; *S. demissum*, 1295; *S. papita*, 1473; and *S. stoloniferum*, 1293.

Virus Content.—Tests for possible virus content were carried out by (*a*) direct examination for symptoms, (*b*) serological tests for viruses X and S, (*c*) sap transfers to differential forms of *S. demissum* for the detection of viruses of the Y group, and (*d*) sap transfers to tobacco, var. White Burley. As a result of these tests 21 lines of the 214 lines examined were found to be infected. One line was infected with viruses S and Y and there were seven infections with virus X, three with virus S, four with virus Y and six with virus A. Many of these infections, ten in all, occurred in *S. tuberosum* material and only five infections were found in wild forms received direct from the collecting grounds. The remaining six infections, five of which were with virus X and one with virus S, were recorded in the once-grown material and could, therefore, be either original or new infections. In serological tests strong non-specific reactions were recorded in various lines of the two species *S. bulbocastanum*, 1617, 1789, 1938 and 1628, and *S. sambucinum*, 1438 and 1668. All infected plants were destroyed, most of them without being tested for reactions to infection with other viruses.

Reaction to Viruses.—Reactions to virus X, S and Y were observed on plants to which the viruses were introduced by sap inoculations, from infected tobacco in the case of virus X and virus Y and from infected Arran Victory potato in the case of virus S. Lines which became systemically infected in consequence of these inoculations were considered to be susceptible and were not examined further. The criteria of infection were (*a*) the production of systemic symptoms and (*b*) recovery and identification of the viruses in appropriate serological or biological tests. Plants which showed no symptoms, or local symptoms only, after sap inoculation were further tested by grafting on to them scions from infected cultivars.

In susceptible lines, virus X gave rise to mosaic symptoms of varying degrees ranging from almost imperceptible mottles to strong necrotic mosaics. Lines showing other reactions were found only in *S. tuberosum* in which 1303 was typically hypersensitive and lines 1670, 1780, 1787, 1860, 1861, 1874 and 1915 appeared to be immune. Slight indications of necrotic responses were recorded in lines of 1550 but the main reactions were indicative of immunity from virus X.

All lines tested were susceptible to virus S. In general there were no observable symptoms in response to infection with this virus but occasionally slight mottles were seen. None of the lines reacted sufficiently clearly, however, to suggest that it might be useful as a diagnostic host for the virus.

Reactions to virus Y covered a wide range of symptoms which, among the lines indicated in the Table as susceptible, varied from light diffuse mottles to typical leaf drop streak and to very severe necrotic mosaics. There were, however, a large number of lines which produced either no symptoms or localised necrotic symptoms on infection by sap-inoculation. On infection by graft all of them reacted with a lethal necrosis, usually of a systemic character. The *S. bulbocastanum* line, 1627, showed very little necrosis and could be described as giving an immune reaction with indications of necrosis. All lines of *S. ehrenbergii* responded with necrotic reactions to virus Y and similar reactions were recorded in *S. bulbocastanum*, *S. cardiophyllum*, *S. jamesii*, *S. michoacanum*, *S. pinnasectum* and *S. stoloniferum*.

Chromosome numbers.—At the request of Professor Hawkes the somatic chromosome numbers of various lines were ascertained. These numbers are given in the final column of the Table.

Series	*Species*	*Collection Number*	*Lines examined*	*Virus content*	*Reaction to viruses*			*Remarks*
					X	S	Y	
III	*S. morelliforme*	1809	4	nil	–	–	–	
IV	*S. bulbocastanum*	1565	1	X	S	–	–	
		1617	3	nil	S	S	SN	
		1627	3	nil	S	S	I(N)	
		1717	1	nil	S	S	N	
		1719	1	nil	S	S	N	
		1789	4	nil	S	S	S	
		1796	1	X	S	–	S	
		1938	5	nil	S	S	S	
	do. *subsp. dolicophyllum*	1628	1	nil	S	S	N	
		1632	2	nil	S	S	S	
		1637	1	nil	S	S	N	
	S. clarum	1776	5	nil	–	–	–	2n = 24
		1777	3	nil	–	–	–	2n = 24
		1778	6	nil	–	–	–	2n = 24
		1813	2	nil	–	–	–	
		1824	7	nil	–	–	–	
		1827	5	nil	–	–	–	
		1894	6	nil	–	–	–	
V	*S. cardiophyllum*	1402	1	nil	S	S	N	
		1598	1	nil	S	S	N	
	do. *subsp. lanceolatum*	1640	1	nil	S	S	–	
		1729	1	S	S	S	S	
	S. ehrenbergii	1440	1	nil	S	S	N	
		1458	3	nil	S	S	N	
		1459	3	nil	S	S	N	
		1462	3	nil	S	S	N	
		1466	1	nil	S	S	N	
		1492	1	nil	S	S	N	
		1494	3	nil	S	S	N	
	S. sambucinum	1438	1	nil	S	S	S	
		1667	1	nil	S	S	S	
		1668	4	nil	S	S	S	

Series	Species	Collection Number	Lines examined	Virus content	Reaction to viruses			Remarks
					X	S	Y	
VI	*S. brachistotrichum*	1234	3	nil	S	S	S	2n = 24
		1471	3	A(1)	S	S	–	
	S. jamesii	1143	3	nil	S	S	–	
		1152	1	X	S	S	–	
		1176	2	nil	S	S	S	
		1197	1	nil	S	S	N	
		1201	1	nil	S	S	N	
		1207	1	X	S	S	N	
		1212	3	nil	S	S	S	
	S. michoacanum	1517	1	nil	S	S	N	2n = 24
		1541	1	nil	S	S	S	2n = 24
	S. pinnatisectum	1665	4	nil	S	S	N	
XII	*S. brachycarpum*	1547	2	nil	S	S	S	2n = 72
	S. semi-demissum	1675	5	S(2)	S	S	S	2n = 60
	S. verrucosum	1374	1	nil	S	S	S	
		1542	1	nil	S	S	S	
		1545	2	nil	S	S	S	
		1345	1	X	S	–	–	
		1350	1	nil	S	S	S	
XIII	*S. fendleri*	1156	5	nil	S	S	SN	
		1157	3	nil	S	S	S	
		1158	5	nil	S	S	SN	
		1160	1	nil	S	S	–	
		1172	4	nil	S	S	S	
		1173	1	A	S	–	–	
		1174	4	nil	S	S	SN	
		1180	3	nil	S	S	S	
		1204	3	nil	S	S	S	
		1209	1	nil	S	S	–	
		1216	1	nil	S	S	S	
		1230	1	nil	S	S	S	
		1259	1	nil	S	S	–	
		1314	1	nil	–	S	–	
	S. hjertingii	1355	1	nil	S	S	–	
		1356	1	nil	S	S	S	
		1357	3	nil	S	S	S	
		1373	3	nil	S	S	S	
		1378	1	nil	S	S	–	
		1379	1	nil	–	–	–	
	S. papita	1475	1	nil	S	S	S	
		1482	2	nil	S	S	S	
		1488	1	nil	S	S	S	
	S. polytrichion	1461	1	nil	S	S	S	
		1465	2	nil	S	S	S	
		1468	1	nil	S	S	S	

Series	*Species*	*Collection Number*	*Lines examined*	*Virus content*	*Reaction to viruses*			*Remarks*
					X	S	Y	
XIII	*S. stoloniferum*	1301	1	nil	S	S	S	
		1452	3	nil	S	S	N	
	? *S. stoloniferum*	1579	1	nil	S	S	N	
		1580	1	nil	S	S	S	
	S. vallis-mexici	1672	1	X	S	–	–	
		1673	4	A(1)	S	S	S	2n = 36
XVII	*S. tuberosum*	1303	1	nil	N	S	N	
		1304	1	X	S	S	S	
		1305	1	A	S	S	S	
		1369	1	nil	S	S	S	
		1534	1	nil	S	S	S	
		1550	3	nil	I(N)	S	S	
		1599	1	A	S	S	S	
		1600	1	nil	S	S	S	
		1670	5	nil	I	S	S	
		1780	5	A(1)	I	S	S	
		1787	1	Y	I	S	S	
		1788	1	Y	S	S	S	
		1858	1	SY	S	S	S	
		1860	1	Y	I	S	S	
		1861	1	Y	I	S	S	
		1874	1	nil	I	S	S	
		1915	1	nil	I	S	S	

A(1) etc. = Virus recovered and number of lines infected
I = Immune
I(N) = Immune with indication of necrosis
N = Necrotic response indicative of hypersensitivity and resistance
SN = Susceptible with necrotic response
S = Susceptible
2n = Somatic chromosome number.

A HOLDER FOR A HYPODERMIC SYRINGE FOR THE RAPID AND ACCURATE DELIVERY OF UNIFORM SMALL DOSES OF INOCULUM

D. Cameron and D. W. Speed

Inoculation experiments at the Scottish Plant Breeding Station in connection with the breeding of oats resistant to the oat stem eelworm *Ditylenchus dipsaci* (Kühn) require an injection into each seedling of approximately 1/500th c.c. of inoculum. To facilitate this an adapter to hold a hypodermic syringe was necessary which would permit a minute downward movement of the plunger for each dose.

Initially a holder which required manual pressure to deliver the dose was used, but since over 1,000 seedlings are inoculated in each test batch, the manual fatigue experienced necessitated a design in which the thrust would be provided mechanically. A satisfactory holder was constructed in which a platform sliding between fixed rails and driven by a screw, applied the thrust to the stem of the syringe.

After several years of intensive use the moving parts are becoming worn, and in view of the possibilities of using the quantitative data obtained from these experiments for genetic analyses, an improved syringe holder is now under construction incorporating the best features of the old, designed to provide a greater uniformity of dose.

The accompanying diagram shows the essential features to be :—a body consisting of a length of tube with an internal thread ; a screwed plug (C) in which a key-way (D) has been cut ; a key (B) screwed to a rotating head (A) with sockets ; a spring-loaded plunger (G) which by engaging in the sockets determines the dose.

The cap (F) of a standard hypodermic syringe is welded to a short plug which is screwed into one end of the body of the holder and the flat thumbpiece of the syringe stem (E) is milled away to terminate in a cone, which rests in a depression in the lower end of the moving plug (C). The size of the dose delivered depends on (*a*) the number of threads per inch in the body and plug ; (*b*) the number of sockets in the rotating head and (*c*) the diameter of the barrel of the syringe which the holder is made to fit. The greatest accuracy is obtained by using the maximum practical number of threads per inch in conjunction with the minimum practical barrel diameter and number of sockets in the head.

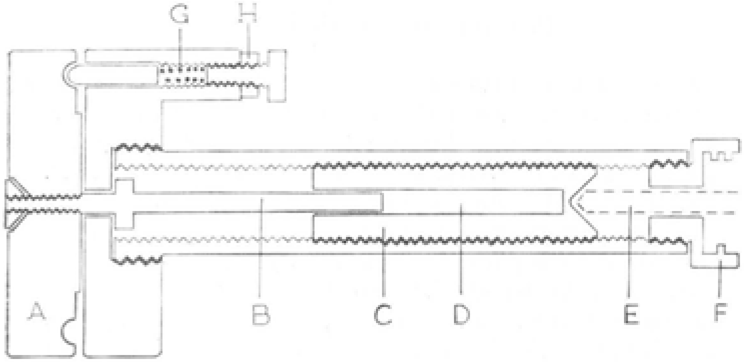


DIAGRAM OF SYRINGE HOLDER

A. Rotating head.
B. Key.
C. Screwed plug.
D. Key-way.
E. Syringe stem.
F. Syringe cap welded to short plug.
G. Spring-loaded plunger.
H. Lock nut.

SOIL ANALYSIS FOR GENECOLOGICAL PURPOSES

Denis Ratcliffe

Introduction

This paper is a preliminary report of investigations on a small area of flushed grassland on the slopes of Carnethy Hill, one of the Pentland Hills south of Edinburgh. The ultimate aim is to find out which environmental factors are determining the distribution of various grass species ; this in turn is part of the wider programme of the Genecology and Herbage Plants section designed to give information on various aspects of hill grassland ecology and genecology with the ultimate aim of formulating methods of improvement.

In this context "flushed" areas (*i.e.* areas naturally irrigated with base-rich water) are of particular significance, for they provide on a single site every gradation from a dense (and closely-grazed) sward of apparently base-demanding species on a rich brown earth of moderate to high pH., to an unproductive "grass-heath" of base-avoiding unpalatable species on well-developed humus podsols with a low pH. There is, therefore, a convenient environmental gradient along which there is a change of vegetation and along which each species reaches the limit of its tolerance at some point or other. It will be shown that there is a particularly striking gradient in the cation exchange capacity of the soil which has a strong effect on the amount of exchangeable cations ; this raises the question of whether the latter is a soil property of intrinsic physiological (and hence ecological) significance to the plant. Moreover, this problem applies to all conditions in which comparison of the availability of cations in soils of different physical composition needs to be made. In fact, on this wider scale the problem is more acute for not only the amount but the type of clay and humus may vary. The problem is especially important when one wishes to obtain information on the tolerance of a species to variation in soil nutrient levels as a factor influencing its distribution ; it is obvious that one should measure availability of nutrients in a way which is independent of the physical constitution of the soil.

The area at present under investigation lies at about 1,200 ft. facing west on a slope of c. 20°, and the source of the flushing is a small spring containing c. 0·5 me/1 Ca, c. 0·23 me/1 Mg, c. 0·03 me/1 K and c. 0·3 me/1 Na. This water disappears after running downwards for about 40 ft.

The flush is clearly marked during most of the year as a narrow area of bright green, closely-grazed turf extending for about 90 ft. down the slope amid a fairly uniform grass heath with much *Calluna* and *Vaccinium myrtillus*; it merges into this surrounding vegetation fairly gradually at the lower end but quite suddenly at the lateral margins.

Methods and Results

Samples were taken along three transects: one 100 ft. long running down the centre line of the flush, along which the water runs for about 40 ft.; two horizontal transects at right angles to this at 30 ft. and 60 ft. from the top, crossing the flush and starting and finishing in the grass heath—both about 40 ft. long. The samples were taken with a boring tool giving cylindrical turves about 12 cm. deep and 7 cm. in diameter; this includes the main rooting zone of the turf constituents. The plant material was removed and the soil air-dried, broken up finely by hand, and passed through a 2 mm. sieve. Usually where a distinct humus-stained layer was present this was treated separately. The species present on each sample core were noted, and from these records it was possible to trace the distribution of each species along the transects.

pH measurements with a glass electrode were made on the fresh soils. Estimations of exchangeable Ca, Mg, K and Na were obtained from the air-dry soils by extraction with $^{N}/_{2}$ NH_4NO_3. The results for the main transect are shown in Table I. The trends are easy to see: sampling points at 0 and 5 ft. are above the point of emergence of the water but there is slight flushing, presumably because of capillarity effects, as the soil is usually slightly moist. Water was present at the surface, at the time of sampling, as far as the sampling point at 40 ft. and the pH in this region remains constantly near to 7·0. Below this point the water disappears and the pH falls

TABLE I

Variation of pH, exchangeable Nutrients and C.E.C. along the three transects

Sampling Point (ft.)	pH	Ca	Mg	K	Na	C.E.C.
0	6.1	9.6	1.5	0.54	0.39	20.0
5	6.2	10.0	1.3	0.31	0.61	17.2
10	7.0	6.8	1.8	0.13	0.20	9.7
15	6.8	6.3	2.0	0.18	2.20	9.2
20	6.8	7.4	1.8	0.18	0.24	10.5
25	6.7	9.4	2.5	0.28	0.32	12.2
30	6.8	8.9	2.2	0.28	0.33	16.7
35	6.7	9.6	2.1	0.23	0.28	15.7
40	6.9	9.8	2.3	0.21	0.26	16.0
45	6.7	10.9	3.7	0.37	0.41	21.1
50	6.3	12.3	2.7	0.18	0.28	22.0
55	6.2	12.7	3.5	0.26	0.43	23.4
60	6.0	15.7	3.6	0.41	0.33	25.7
65	6.0	13.7	3.6	0.35	0.43	26.2
70	6.0	14.0	3.2	1.12	0.24	24.9
75	6.0	11.9	3.0	0.33	0.39	23.4
80	5.9	12.3	2.7	0.33	0.26	24.2
85	5.4	9.0	3.4	0.42	0.39	24.7
90	5.1	7.1	1.8	0.44	0.28	24.2
95	4.3	3.0	2.5	0.60	0.30	27.9
30.12L	4.4	4.8	0.5	0.28	0.24	22.7
30.10L	4.6	4.1	1.2	0.38	0.24	21.5
30. 8L	5.1	6.9	2.0	0.55	0.32	22.2
30. 6L	5.4	9.4	1.6	0.48	0.32	22.0
30. 4L	5.9	14.1	3.2	0.51	0.44	24.7
30. 2L	6.4	12.2	2.8	0.38	0.32	20.7
30	6.8	10.0	2.3	0.28	0.33	16.7
30. 2R	6.3	5.9	1.2	0.21	0.31	20.5
30. 4R	5.7	5.9	1.2	0.34	0.28	22.0
30. 6R	4.5	2.3	1.4	0.63	0.24	23.9
30. 8R	4.1	1.2	0.8	0.37	0.19	23.4
60.12L	4.1	0.9	0.5	0.31	0.17	21.2
60.10L	4.4	2.5	1.2	0.48	0.19	26.7
60. 8L	4.5	3.9	1.8	0.67	0.20	23.4
60. 6L	5.2	7.8	2.3	0.66	0.30	22.0
60. 4L	6.0	14.4	3.4	0.64	0.37	23.4
60. 2L	6.0	14.0	2.9	0.36	0.33	22.2
60	6.0	15.7	3.6	0.41	0.33	25.7
60. 2R	5.9	14.0	3.0	0.38	0.39	23.7
60. 4R	5.9	13.6	3.2	0.41	0.34	23.7
60. 6R	4.9	6.4	1.4	0.59	0.28	23.08
60. 8R	4.2	0.9	1.2	0.33	0.13	22.9
60.10R	4.0	0.7	0.7	0.33	0.15	24.3

0 to 95 ft.—Main transect.
30.12L to 30.8R.—Horizontal transect at 30 ft.
60.12L to 60.10R.—Horizontal transect at 60 ft.
12L, 10R etc., denote feet to left or right of main transect.

gradually down the slope and then remains constant until the sample at 75 ft. Beyond this point the effect of leaching is apparent, for the surface soil becomes slightly humus-stained and the pH is lower than at a depth of 10 cm. This trend continues until 95 ft., at which point the soil has the profile of a well-developed podsol with a distinct raw humus layer at the surface.

The trend in the level of calcium is, however, rather different ; there is a *fall* in the sample from 10 ft. followed by a progressive *rise* in successive samples down the flush, as far as 60 ft. then a fairly steep fall to a low level at 95 ft. Magnesium shows a similar but less marked trend. Potassium and sodium show only small variations.

The cause of this pattern of variation was not at first obvious but careful examination of the soil samples suggested that the soils were coarser in the wetter parts and finer in the drier parts, in fact, fine material seems to have been washed by the flush water from the areas through which it was continually seeping, giving a gradient of diminishing coarseness from the wettest to the driest soils ; in addition the humus content of the soil increases away from the flushed area. Since it is well known that clay and humus are responsible for the greater part of the cation exchange capacity (C.E.C.) of a soil it seemed that variation in these would account for the patterns described above. The amount of cations in a flushed soil should be proportional to its C.E.C. It might therefore be expected that the series from coarse- to fine-structured soil would give the trends in Ca and Mg shown by Table I. The effect of leaching explains the fall in exchangeable cations on the soils with a high proportion of humus.

A convenient method for determination of C.E.C. was, therefore, evolved based on the method of Mehlich (1948) and values obtained for all the samples (Table I). The figures show that the C.E.C. rises from the point of emergence of the water to 60 ft. on the transect, then falls off slightly to 90 ft., rising considerably at 95 ft. where the humus content is much higher. On the horizontal transect at 30 ft. the course of the flush water is marked by a low value for C.E.C. but on the horizontal transect at 60 ft. C.E.C. is approximately constant with a slight peak in the centre and higher values where there is a higher humus content. This pattern entirely accounts for the pattern shown for exchangeable Ca and Mg.

Discussion

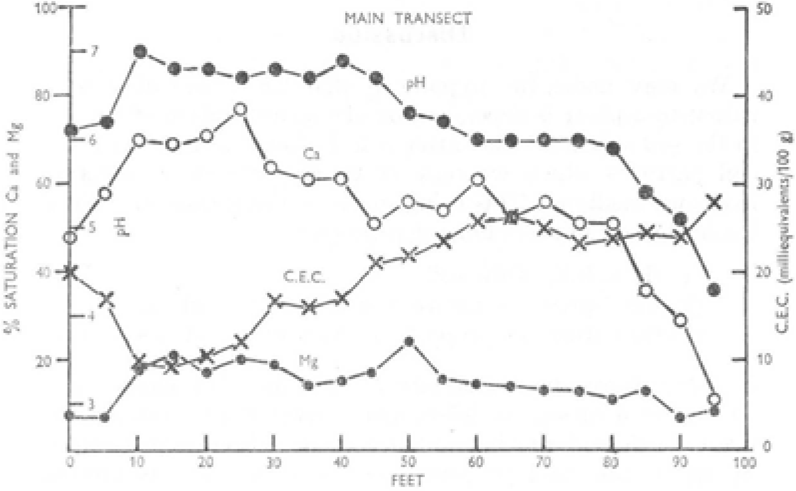
We may make the hypothesis that the availability of a cation to a plant is dependent on the concentration of the ion in the soil solution ; the latter is in intimate contact with the soil particles which we may treat as particles of a cation exchange medium. This being so the concentration of a given ion in the soil solution must depend on :—

(*a*) the C.E.C. of the soil
(*b*) the degree of saturation of the C.E.C. with the ion
(*c*) the nature and proportions of the other cations present.

In other words the availability of the same " exchangeable " amount of a cation (as determined above) will be lower if the C.E.C. of the soil is higher and *vice versa*. This will be modified by the nature and properties of the other cations present (complementary ions), but where the ion under consideration is Ca^{++} it is likely that this effect will be relatively unimportant because Ca usually represents about 50-80 per cent of the cations in soils and the effect of Ca on the *other* ions will be the dominant feature.

Strong evidence that this kind of mechanism does operate has been provided by Jenny and Ayers (1939). They showed that the amount of potassium taken up by excised barley roots from a suspension of clay in dilute solution of KCl depends to a large extent on the degree of saturation with K^+ of the clay. They also showed that K^+ is relatively more available if Ca^{++} rather than Na^+, H^+ or NH_4^+ is present as the complementary ion.

It seems reasonable to conclude that if the amounts of exchangeable cations in the soils under investigation are expressed as a percentage of the relevant C.E.C. then the resulting values would be a much more meaningful measure of cation availability to the plants. This has been done and the results for Ca, Mg, C.E.C. and pH are shown in Figs. 1, 2 and 3. It can be seen that despite varying C.E.C. (crosses) the degree of saturation of Ca (open circles) and Mg (small dots) follows the same trend as pH (large dots). There is also a more clear cut transition from high calcium to low calcium soils, corresponding with a change in pH, which fits the vegetation pattern very well.



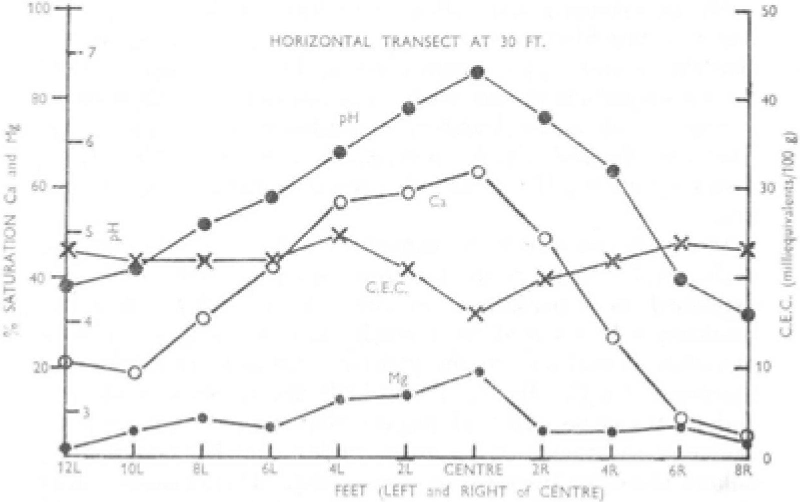


FIG. 1 (*top*), FIG. 2 (*bottom*).—Variation of pH, exchangeable Ca and Mg, and C.E.C.

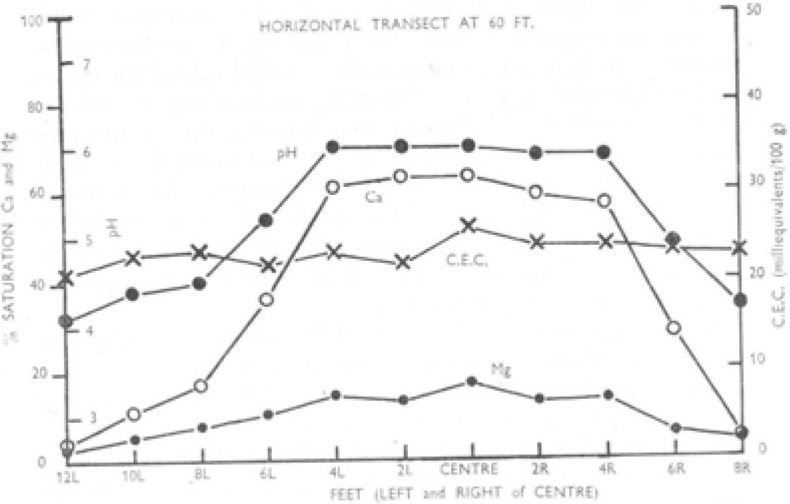


FIG. 3.—Variation of pH, exchangeable Ca and Mg, and C.E.C.

It remains to demonstrate that this method of expressing availability of cations does give a criterion which one can use in assessing its importance in influencing the distribution of individual species. This is not easy, for pH itself has effects unconnected with ion exchange reactions, particularly in relation to the so-called minor and trace elements. In addition independent factors such as soil moisture and aeration may have a masking effect. There is a certain amount of circumstantial evidence from the flush under consideration: the outer limit of *Festuca rubra* seems to correspond to the point at which Ca saturation falls to 20-30 per cent; it is suspected that the inner limit is related to the degree of wetness of the soil.

There is, however, more cogent evidence from another source. Similar analyses were performed on a series of soils collected by a colleague from sites on which *Potentilla erecta* was growing. These came from places as far apart as the Border country and West Sutherland, and from vegetation types as different as *Festuca/Agrostis* grassland and *Molinia* moor. The pH ranges from 3·7 to 6·3 (mostly between 4·4 and 5·2), C.E.C. from 11 to 36 me/100 g., Ca saturation from 10 per cent to 50 per cent (mostly between 15 per cent and 40 per cent). Comparing these figures with Figs. 1, 2 and 3 it is clear that values of this order appear between 80 ft. and 95 ft. on the vertical transect and in bands 4 to 6 ft. wide on either side of the centre of the horizontal transect. *Potentilla erecta* is only present in small quantity on this flushed area (possibly due to the very high grazing intensity) and it does in fact occur in precisely those zones indicated by the above figures; this strongly suggests that availability of Ca in the soil is an important factor influencing its distribution. The prominent species are *Festuca ovina, Agrostis tenuis, Anthoxanthum odoratum* and occasional *Deschampsia flexuosa*.

The comparison of data obtained from soils of such various origins with those obtained from the flushed area, to give such an appropriate prediction lends considerable support to the hypothesis previously outlined.

It is concluded that the results here discussed are sufficiently encouraging to warrant further work in this direction, so that relation between cation availability and the distribution of individual species can be more fully studied.

I wish to express my thanks to Dr Jack Dainty, Department of Biophysics, University of Edinburgh, for invaluable discussion of ion exchange processes.

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NUTRIENT IRRIGATION EXPERIMENTS ON THE ISLE OF RHUM

R. E. C. Ferreira

The Nature Conservancy, Edinburgh

The use of nutrient irrigation as a means of improving Scottish hill grazings has recently been discussed by Gregor (1961). Gregor emphasises the importance of the studies of Heddle and Ogg (1936), who irrigated hill pastures with spring water with considerable success. The present note comments on similar work to be undertaken by the writer on the Isle of Rhum, which will be complementary to the irrigation experiments being carried out by the Scottish Plant Breeding Station on the Pentland Hills.

Rhum, a National Nature Reserve, owned by the Conservancy is well suited to experiments aimed at improving hill grazings by flushing peaty ground with nutrient-rich water. This is because there are large areas of acid, base-poor peat in the northern half of the island overlying Torridonian sandstone that are intersected by burns carrying water of moderate base status. For the initial experiments, one such area has been chosen on the north side of Kinloch Glen where a burn with a reasonably regular water flow traverses peaty ground bearing *Calluna-Scirpus* and *Calluna-Molinia* communities. Analyses of two samples of peat from the *Calluna-Scirpus* community are given in the accompanying table.

Sample	pH	Loss on Ignition	Na	K	Ca	Mg	P	N
1	5·1	48·7	24	38	64	47	0·8	1·66
2	4·5	67·8	25	44	100	46	0·9	1·92

pH 1 : 2·5, soil : water ratio.
Loss on ignition at 550°C as per cent dry wt.
Na, K. Ca, Mg and P as mg/100 gms. dry wt.
N as per cent dry wt.

The burn water which is to be used in the experiment contains 1·2-1·5 mg/l Ca and 1·0-1·2 mg/l Mg. Although the Ca level of this burn would appear to be low it approaches the average Ca content of medium-sized Highland burns. Some indication of the potential of this water for improving the vegetation may be obtained from the observation that the flood water from the burn has at one point flushed the banks about 10 ft. back from the burn where a herb-rich grass heath has developed.

The first aim of this experiment is to find out to what extent the base status and pH of the peat are raised by irrigation over a given time period. Secondly, the change in the floristic composition of the vegetation is to be observed during a period of several years. The latter change may well be much slower due to the fact that the nearest source of species that would grow on the " improved " peat is some 300 yards distant. It is appreciated that any improvement in the vegetation in an area such as this would be slight by comparison with that on ground irrigated with spring water arising directly from strongly calcareous rocks. Nevertheless, if an improvement can be demonstrated by irrigation from burns arising on Torridonian sandstone then the experiment has been worthwhile.

The burn is to be dammed this spring (1963) at a point where a good head of water can be obtained. From the dam, ½" polythene piping will lead the water on to the *Calluna-Scirpus* community and it will be dispersed over the ground by boring holes at regular intervals along the lower part of the pipe and sealing the end. In order to allow the establishment of new species in the irrigated areas it will be necessary to restrict irrigation to certain seasons of the year. It seems to the writer to be best to apply the water during the winter months (which are relatively frost-free in the Hebrides), prior to the spring growth. However, should there be a severe drought during the spring or early summer, further intermittent irrigation would then be needed.

At a later date it is planned to set up similar experiments in the area of ultrabasic rock in the southern half of the island. Irrigation with Ca-rich water should prove particularly beneficial to the *Calluna* and grass heath communities developed on the Mg-rich soils derived from peridotite. In this connection it may be noted that one of the chief sources of *Agrostis-Festuca* grassland in the area is found on the margins of the burns flushed by Ca-rich water, which arises from the dolomitic peridotites. After the initial results have been obtained from experiments employing natural water, additional nutrients will then be added prior to irrigation in both the Torridonian and ultrabasic schemes. Pilot experiments employing direct applications of Ca, N and P to the *Calluna-Scirpus* and other acidophilous plant communities are to be started in 1964 to facilitate the choice of fertilizers to be added to the irrigation water.

The writer would like to thank Miss M. C. Gray and Mr S. E. Allen of the Nature Conservancy for the soil and water analyses.

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THE SCOPE AND PROBLEMS INVOLVED IN SYNTHESISING NEW AMPHIDIPLOID AND AUTO-TETRAPLOID FODDER BRASSICAS IN THE GROUP *B. NAPUS* L., *B. CAMPESTRIS* L. AND *B. OLERACEA* L.

I. H. McNaughton

The cytogenetic relationship of *B. napus* (2n = 38) to *B. campestris* (2n = 20) and *B. oleracea* (2n = 18) was first realised by U (1935) but it is only comparatively recently that the range of variability in *B. napus* has been improved through the production of artificial forms of practical value. Synthetic swedes have been produced by Rudorf (1950), Koch and Peters (1953) and by Olsson *et al* (1955); oil-seed rape forms by Frandsen (1947) and Olsson (1960); leafy types by Hosoda (1950) and Nishi *et al* (1959). In view of the very wide range of variation within *B. campestris* and within *B. oleracea* there seems to be ample opportunity for synthesising new amphidiploids (*i.e.*, *B. napus*) which may be useful as fodder plants.

Natural B. napus.

B. napus may have originated spontaneously where the distribution of *B. campestris* and *B. oleracea* overlap. According to Sinskaia (1928), wild *B. campestris* is widespread from Western Europe to Eastern Asia, whilst *B. oleracea* has its natural distribution along the Atlantic coast of Western Europe and in the Mediterranean region. Rudorf (1950) and Olsson (1954a) have assumed *B. napus* to have originated several times involving different forms of the parental species. In spite of the overlapping geographic distribution of *B. campestris* and *B. oleracea* the existence of wild forms of *B. napus* is in some doubt. This is partly due to the difficulty in distinguishing true wild types from escapes from cultivation.

Cultivated forms of B. napus

Several forms of *B. napus* are already well known in cultivation. Firstly there is the swede *B. napus* ssp. *rapifera* (Metzg.) Sinsk., (*B. napobrassica* (L.) Mill.) of which numerous cultivars exist, these vary in colour and shape of " bulb " and in leaf form. Most are fairly frost resistant but are normally lifted and used as cattle fodder in the autumn. They are sometimes left in the field to be grazed by sheep. Swedes, of course, are also used for culinary purposes. In the winter rape, *B. napus* var. *biennis* (Schuebl. and Mart.) Reichenb., there are both oil-seed and fodder forms. Oil-seed rape, widely grown on the Continent for use in the manufacture of margarine, is higher yielding than oil-seed turnip rape (*B. campestris* ssp. *oleifera* (Metzg.) Sinsk., and in Scandinavia is generally used in preference to it where hardiness is not a primary consideration. Summer rape (*B. napus* var. *annua* Koch.) contains only early maturing oil-seed forms.

Rape is often grown as a fodder crop for both sheep and cattle and there are several well known cultivars. " Broad-leaved Essex rape " is low growing and leafy but not as high yielding as some of the taller growing giant rape forms. The leaf/stem ratio of giant rape is, however, fairly low and the overall palatability probably less, especially late in the season. Johnston (1961) compared the yields of several *B. napus* varieties: giant rape, dwarf rape, hungry-gap kale, asparagus kale and rape kale. Giant rape gave the highest total yield but its yield of leaf was no greater than dwarf rape or hungry-gap kale. *B. napus* and *B. oleracea* forms are frequently grouped together as " kales " in seedsmen's catalogues. To avoid confusion it would seem sensible to apply the term " kale " to *B. oleracea* only. A selected form of giant rape 'New Zealand Club-root Resistant', as the name implies, shows some resistance to *Plasmodiophora* but is by no means immune. A recent development from New Zealand is an aphid resistant rape, this may be of considerable importance in hotter, drier climates but may not be of much practical value in Britain. The culture and utilisation of fodder rape is described by Symons (1961). *B. napella* (Chaix), sometimes called " oriental rape ", is apparently completely interfertile with *B. napus* (Olsson, 1954a).

The synthesis of B. napus

Several methods of producing synthetic and semi-synthetic *B. napus* have been outlined by Hoffmann and Peters (1958), four of these are listed below. Other methods are of relatively minor interest and are only essentially different in that use is made of natural unreduced gametes instead of artificial chromosome doubling agents.

TABLE I(A)

INTERSPECIFIC HYBRIDISATION INVOLVING B. CAMPESTRIS AND B. OLERACEA

♀ 2*x* B. campestris		× ♂ 2*x* B. oleracea		*No. of flowers pollinated*	*Total seed obtained*	*No. of seeds germinated*	*Parthenogenetic plants*	*True Hybrid plants*	*Special techniques applied*	*Investigator*	*Date*
subspecies	*cultivar*	*variety*	*cultivar*								
?		?		732	26	—	11	4*	Straight pollination	U. Nagahara	1935
chinensis		*capitata*		122	0	—	—	—	" "	Karpechenko	1937
oleifera		*acephala* *gemmifera* *capitata*		7,434	3,994	—	—	15	" "	Olsson	1949-57
rapifera				2,961	793	—	—	1	" "	"	1952-55
oleifera	'Lembkes'	*acephala*		1,462	18	—	—	—	" "	Hoffmann and Peters	1953
"	'Grubers'	*gemmifera*		2,326	92	57	—	12	" "	" "	1954
rapifera		*capitata*		3,956	144	72	—	3	" "	" "	1955
				575	356	115	—	5	" "	" "	1956
				61	0	0	—	—	" "	" "	1957
rapifera	'Shōgoin-Kabu'	*gongylodes*		28	112	112	103	6	Grafted to *B. campestris* ssp. *rapifera* 'Shōgoin-Kabu'	Hosoda	1960
"	"	"		17	54	54	54	0	Straight pollination	"	1960
rapifera *oleifera*	6 vars.	*capitata* *gongylodes*		214	3	—	—	0	" "	"	1960
"	"	"		69	2	2	—	2	Boric acid 100 p.p.m. applied at pollination	"	1960
"	"	"		55	—	—	—	—	Boric acid 50 p.p.m. applied at pollination	"	1960
"	"	"		65	—	—	—	—	Straight pollination	"	1960
pekinensis		*acephala*	'Siberian Kale'	'Many'	0	—	—	—	" "	Honma and Heeckt	1960
"		"		?	5	—	—	5	N-m-Tolyl-Thalamic acid applied at pollination	" "	1960
rapifera		*gongylodes*		206	0	—	—	—	Straight pollination	" "	1960

* Plants with 2n = 19, 28, 29 and 38 chromosomes respectively.

TABLE I(B)

♀ 2x B. oleracea *variety*	*cultivar*	×	♂ 2x B. campestris *subspecies*	*cultivar*	*No. of flowers pollinated*	*Total seed obtained*	*No. of seeds germinated*	*Parthenogenetic plants*	*True hybrid plants*	*Special techniques applied*	*Investigator*	*Date*
capitata			*chinensis*		70	0	—	—	—	Straight pollination	Karpechenko	1937
acephala			*rapifera*		107	—	—	—	—	" "	Calder	1937
capitata			"		132	0	—	—	—	" "	Becker	1946
acephala *gongylodes*			*oleifera*		2,456	246	—	—	0	" "	Olsson	1949-56
"			*rapifera*		281	—	—	—	1	" "	Becker	1951
acephala *gongylodes*			"		1,618	100	—	—	0	" "	Olsson	1953-55
acephala			*oleifera*	'Lembkes'	3,592	1	0	—	0	" "	Hoffmann and Peters	1954
gemmifera			"	'Grubers'	4,728	7	5	—	0	" "	" "	1955
capitata			"		1,383	299	64	—	0	" "	" "	1956
gongylodes			"		921	12	10	—	*	" "	" "	1957

* Not ascertained

TABLE I(C)

♀ 4x B. campestris *subspecies*	*cultivar*	×	♂ 4x B. oleracea *variety*	*cultivar*	*No. of flowers pollinated*	*Total seed obtained*	*No. of seeds germinated*	*Parthenogenetic plants*	*True hybrid plants*	*Special techniques applied*	*Investigator*	*Date*
	?		*capitata*	'Erstling'	3,000	—	—	—	37	Straight pollination	Frandsen	1947
oleifera	'Lembkes'		*cephala*		13,867	2,246	—	—	129	" "	Olsson	1948-57
"	'Wilnensis'		*capitata*									
"	'Grubers'		*fimbriata*									
"	"		*gemmifera*									
rapifera			*acephala*		9,017	1,105	—	—	4	" "	"	1952-55
"			*capitata*									
"			*fimbriata*									
oleifera	'Lembkes'		*capitata*		2,833	9	0	—	0	" "	Hoffmann and Peters	1953
"	'Wilnensis'		*acephala*		2,339	5	3	—	0	" "	" "	1954
"	"		*gongylodes*		3,081	2	0	—	0	" "	" "	1955
"	"		"		1,458	7	3	—	0	" "	" "	1956
"			"		276	?	—	—	0	" "	Hosoda	1960

TABLE I(D)

♀ 4x B. oleracea variety	♀ 4x B. oleracea cultivar	×	♂ 4x B. campestris subspecies	♂ 4x B. campestris cultivar	*No. of flowers pollinated*	*Total seed obtained*	*No. of seeds germinated*	*Parthenogenetic plants*	*True hybrid plants*	*Special techniques applied*	*Investigator*	*Date*
acephala *capitata* *fimbriata* *gemmifera*			*oleifera*		12,190	1,048	—	—	130	Straight pollination	Olsson	1948-57
			rapifera		6,684	387	—	—	0	,, ,,	,,	1952-55
gongylodes *capitata* *acephala*			*oleifera*	'Lembkes' 'Wilnensis'	2,326	0	—	—	—	,, ,,	Hoffmann and Peters	1953
			,,		3,093	1	1	0	1	,, ,,	,, ,,	1954
			,,		1,124	0	—	—	—	,, ,,	,, ,,	1955
			,,		597	1	—	—	—	,, ,,	,, ,,	1956

Method 1

> *B. campestris* (2n = 20) aa × *B. oleracea* (2n = 18) cc and reciprocal F_1 treated with colchicine = *B. napus* (2n = 38) aacc, synthetic.

This method has been the most commonly used in synthetic *B. napus* production and numerous cultivars of both *B. campestris* and *B. oleracea* have been tried as parents. (Results of several workers are listed in Table 1a and b.) Success appears to vary depending on which species is female parent. When *B. campestris* was used 48 hybrids resulted from 20,283 pollinations but with *B. oleracea* only one hybrid was obtained following 15,288 pollinations.

The particular cultivar and strain employed in crossing may be important. Thus Olsson (1960) obtained 15 hybrids from 7,434 crosses in which turnip-rape was the female parent but only one hybrid from 2,961 crosses where turnip was used. The genotype of the particular individuals within each strain may also be important. This point has been stressed by Olsson (*loc. cit.*) who found that most of the hybrid seeds were harvested from a few female plants although many were used in his experiments.

The F1 hybrid *B. campestris* × *B. oleracea* (2n = 19) and its reciprocal is highly sterile. A plant studied by U (1935) had only 7·4 per cent good pollen. Chromosome pairing in such a hybrid appears to vary from cell to cell but generally few bivalents are formed. The restoration of fertility through chromosome doubling has been successfully achieved by colchicine. This is best carried out on cloned material so as to increase the chances of success. U (*loc. cit.*) found one spontaneously doubled hybrid following crosses at the diploid level.

Method 2

> 4x *B. campestris* (2n = 40) aaaa × 4x *B. oleracea* (2n = 36) cccc and reciprocal F_1 treated with colchicine = *B. napus* (2n = 38) aacc, synthetic.

Greater success in producing hybrids between *B. campestris* and *B. oleracea* may be achieved by crossing the species at the tetraploid level. Olsson (1960) obtained only 16 hybrids from 14,469 crosses involving 2x *B. campestris* and 2x *B. oleracea* but 263 hybrids resulted from 41,758 pollinations between tetraploids. Olsson suggests, however, that different strains of the parental species may be just as important as ploidy in influencing success or failure.

One advantage in crossing the species at the tetraploid level is that a fertile amphidiploid is immediately obtained, whereas crossing at the diploid level produces a highly sterile F1 hybrid which must then be treated with colchicine to restore chromosomal balance and fertility. There are exceptions to this generalisation in that occasional aneuploids may result from intercrossing tetraploids whilst crossing between diploids may produce an amphidiploid through pairing of unreduced gametes (see, for example, U, 1935).

The advantages of crossing at the tetraploid level can be seen when the results of attempts by several investigators (U, 1935; Calder, 1937; Karpechenko, 1937; Becker, 1951; Frandsen, 1947; Hoffmann and Peters, 1958; Honma and Heeckt, 1960; Hosoda, 1961; Olsson, 1960) are combined. The number of pollinations required to produce a hybrid is considerably greater at the diploid level, especially where *B. oleracea* is used as female parent.

Cross	*Pollinations per hybrid*
2x *B. campestris* × 2x *B. oleracea*	432
4x ,, × 4x ,,	211
2x *B. oleracea* × 2x *B. campestris*	15,288
4x ,, × 4x ,,	199

The data suggest that there is no great advantage as to which species is used as female parent in crosses at the tetraploid level. It may be more convenient to use *B. oleracea* as seed parent in view of its larger flowers which are more easily emasculated and pollinated.

Method 3

(*a*) *B. napus* (2n = 38) aacc × *B. campestris* (2n = 20) aa F_1 treated with colchicine = *B. napocampestris* (2n = 58) aaaacc.

(*b*) *B. napocampestris* (2n = 58) aaaacc × *B. oleracea* (2n = 18) cc = *B. napus* (2n = 38) aacc, semi-synthetic.

The initial cross between *B. napus* and *B. campestris* is more readily made when *B. napus* is the female parent. The F1 hybrid (2n = 29), which is almost entirely sterile, can be produced in large enough quantities to allow mass treatment of seedlings with colchicine. Hoffmann and Peters (1958) obtained 23,596 seed from 17,484 pollinations in crosses between *B. napus* "Lembke's rape" and *B. campestris* ssp. *rapifera* (turnip) but other subspecies of *B. campestris* seem to be equally successful as pollen parents (see Table 2).

TABLE 2

♀	♂	*Pollinations*	*siliquas*	*seed*	*seed/sil*
B. napus	*B. campestris* ssp. *rapifera*	162	65	344	5·3
,,	,, ssp. *oleifera*	83	30	304	10·1
,,	,, ssp. *chinensis*	25	?	103	—
,,	,, ssp. *nipposinica*	289	160	1,310	8·2
,,	,, ssp. *pekinensis*	32	15	146	9·7

B. napocampestris (2n = 58), first described by Frandsen and Winge (1932) in a cross *B. napus* "Bangholm" swede × *B. campestris* "Yellow Tankard" turnip, may be considered an auto-allo-hexaploid. Plants of similar genomic constitution examined by the author were low in fertility and meiotic behaviour was somewhat irregular. Occasional quadrivalents and univalents were observed at M_I in CO plants whilst at A_{II} segregation was not entirely regular. Eighty-two cells out of 159 examined at M_{II} showed 29 chromosomes on one or both plates. Aneuploids with chromosome numbers ranging around 2n = 58 were found in later generations.

The seed yield of *B. napocampestris* is generally low, nevertheless fertility seems to vary between individuals and it should be possible to improve the amount of seed set through selection. Six hundred and ninety-eight hand pollinations between C1 plants produced 320 siliquas and 460 seeds. The mean number of seeds per siliqua was 1·4, but some plants yielded an average of up to 3·5 seeds per siliqua. A higher seed yield was obtained by open pollination between plants in isolation.

The F1 hybrids *B. napus* × *B. campestris* ($2n = 29$) although highly sterile, may have some future as a fodder crop provided the right combination of parents is used. Such a hybrid obtained by crossing an artificial *B. napus* with *B. campestris* ssp. *pekinensis* is reported by Hinata (personal communication) to be highly productive and palatable and to have aroused considerable interest among horticulturalists in Japan. Seed can be produced on a commercial scale by utilising self-incompatibility in *B. napus*. This method may yield sufficient seed for use as a horticultural crop but perhaps not on the larger scale required by agriculture. Hybrids involving *B. napus* ('Broad leaved Essex rape' and giant rape) and the oriental forms *B. campestris* ssp. *nipposinica* and *chinensis* (produced at Pentlandfield) possessed good leafiness and frost resistance.

B. napocampestris ($2n = 58$) × *B. oleracea* ($2n = 18$) should theoretically give *B. napus* ($2n = 38$) which in this case could be called "semi-synthetic". However, as Hoffmann and Peters (1958) have shown, this cross may be very difficult, only three confirmed hybrids being obtained from 13,566 pollinations. This method illustrates how the genetic constitution of *B. napus* may be improved through the introduction of new factors from *B. campestris* and *B. oleracea* but the chromosome unbalance of *B. napocampestris* and the difficulty in making the second cross suggest that it may be only of academic interest.

Method 4

(*a*) *B. napus* ($2n = 38$) aacc × *B. oleracea* ($2n = 18$) cc F_1 treated with colchicine = *B. napoleracea* ($2n = 56$) aacccc.

(*b*) *B. napoleracea* ($2n = 56$) aacccc × *B. campestris* ($2n = 20$) aa = *B. napus* ($2n = 38$) aacc, semi-synthetic.

This method, although theoretically possible, seems even more impracticable than the preceding one. In this case the initial cross, as well as the second cross, is difficult to effect. Hoffmann and Peters (1958) obtained only 32 confirmed hybrids from 8,708 pollinations of the cross *B. napus* × *B. oleracea* and no hybrids resulted from crossing the amphidiploid *B. napoleracea* ($2n = 56$) with *B. campestris* (2,181 pollinations).

Mizushima is reported by Hosoda (1961) to have made the cross *B. campestris* 'Chīfūhakasai' × *B. oleracea* 'Succession' and obtained a hybrid 2n = 28 (acc), probably through the pairing of an unreduced gamete from *B. oleracea* with *B. campestris*. The amphidiploid (*B. napoleracea*) was derived by means of colchicine. This gave rise to heteroploid progeny. After repeated selfing Hosoda (loc. cit.) was able to select new strains with 2n = 38 chromosomes (*i.e. B. napus*). These are reported to be winter hardy in Japan and to have grown luxuriantly in early spring.

The variation within B. campestris L.

B. campestris (*sensu lato*) is a large and polymorphic species. The group has recently been revised by Olsson (1954b) to include *B. rapa* (L.) (the turnip) and the oriental species *B. chinensis* (L.) Makino, *B. narinosa* Bailey, *B. nipposinica* Bailey (which probably corresponds to "*B. japonica*" Sieb), and *B. pekinensis* Ruprecht. All these "species" have been shown to be completely interfertile, although some hybrids involving ssp. *trilocularis* (yellow-seeded "sarson") showed reduced fertility (Olsson, 1954b). The diversity of forms within this group has been used for different purposes, the seed in the manufacture of margarine, the leaves and "bulbs" as fodder for animals and for culinary purposes.

B. campestris ssp. *oleifera* (Metzg.) Sinsk., is better known as the oil-seed turnip rape. There are numerous cultivars, mostly showing only slight variation, but there are annual and biennial forms. Turnip-rape is sometimes used as fodder, winter forms have been shown to have greater frost resistance than rape (Torssel, 1959) and are consequently favoured in more northerly regions of Scandinavia.

Ssp. *rapifera* (Metzg.) Sinsk., formerly *B. rapa* (L.), the turnip, is well known as a vegetable and as a fodder crop. Many cultivars exist differing in "root" shape, colour and leaf form. Most have lyrate leaves but in a few such as 'Gelria' the leaves are entire. Some cultivars, notably 'Bruce', 'Wallace', several Dutch turnips and the Swedish 'Immuna' are fairly resistant to *Plasmodiophora brassicae* Woron. (clubroot). Resistance is considered to be due to multiple genetic factors (Tedin, 1932). The turnip is normally biennial.

Ssp. *chinensis* (L.) Makino, is a leafy, quick growing annual which forms compact, elongate heads consisting principally of swollen, white, leaf mid-ribs and petioles which are considered a delicacy in Eastern Asia. When grown under normal conditions in Britain ssp. *chinensis* flowers early and shows very little tendency to form hearts. All forms examined at Pentlandfield were susceptible to frost. Ssp. *chinensis* is relatively low in dry matter, all above ground parts of the plant are likely to have a dry matter percentage of 7-8 per cent. The fleshy mid-ribs and petioles if analysed separately may have a dry matter of as low as 3·5 per cent.

Ssp. *nipposinica* (Bailey) Olsson. There appear to be two forms of this subspecies, one with numerous strap-shaped, entire leaves, the other with finely dissected leaves. Both form a dense rosette and do not show the same tendency towards early flowering as do ssp. *chinensis* and ssp. *pekinensis*. Ssp. *nipposinica* is not winter hardy in Britain and like other oriental brassicas is fairly highly susceptible to club-root. The dry matter content of all the above ground parts of the plant, consisting almost entirely of leaves, is around 7 per cent.

Ssp. *pekinensis* (Lour.) Olsson. The chinese cabbage has pale yellow-green leaves, which are broad and entire, sometimes with a dentate margin. In the Orient it forms large, compact hearts but these seldom develop under normal conditions in Britain. Some cultivars form vigorous, leafy plants but there is a tendency to flower early from spring sowing. The dry matter is comparatively low, around 7 per cent, and like the other oriental subspecies *pekinensis* is not winter hardy in Britain.

Ssp. *narinosa* (Bailey) Olsson. Like the other oriental forms ssp. *narinosa* is used as a vegetable in eastern Asia and forms a tight rosette of rather small, dark green, entire leaves which are puckered or crumpled.

Ssp. *dichotoma* (Roxb.) Olsson. Commonly called toria this subspecies is normally used in India as an oil-seed plant. It flowers very early from spring sowing, leaf development is poor and most of the leaves remaining at maturity are small and cauline.

Ssp. *trilocularis* (Roxb.) Olsson. The yellow-seeded sarson is also frequently cultivated in India for oil-seed. Leaf development is normally poor and if sown in early summer in Britain it soon runs to seed.

The variation within B. oleracea L.

The variation in *B. oleracea* is perhaps better known than in *B. campestris.* Many so-called "varieties" exist, some of them just as distinct, if not more so, as the "subspecies" within the *B. campestris* group. Leaves, swollen stems, modified and axillary terminal buds etc., have all been developed and utilized for different purposes. Some forms have been in cultivation for several hundred years.

B. oleracea var. *sylvestris* L. (wild cabbage)

It is often difficult to distinguish between true wild-types and escapes from cultivation, but the maritime cliff plants occurring along the Atlantic coasts of Europe and round the Mediterranean are most probably true wild forms. These are biennial or perennial with small lyrate leaves and woody stems which are often branched. Wild *B. oleracea* is described in greater detail by Onno (1933) and Gates (1950).

B. oleracea var. *capitata* L. (cabbage)

The modern cabbage has undoubtedly been developed through selection from wild *B. oleracea.* The terminal bud has become enlarged to form a compact head or heart. There is considerable variation in size, shape and consistency of hearts, degree of development of outer leaves, time of maturity etc. A large number of culinary and fodder cultivars exist. The savoy cabbage, sometimes described as *B. oleracea* var. *sabauda L.* is perhaps best considered as a distinct form of var. *capitata* with characteristically puckered or crumpled leaves.

B. oleracea var. *gemmifera* Zenker (brussels sprouts)

The brussels sprout is a biennial characterised by the high degree of development of vegetative buds in the axils of the leaves. Cultivated in the vicinity of Brussels as early as 1213 (Oldham, 1948).

B. oleracea var. *gongylodes* L. (kohl-rabi)

Kohl-rabi consists of a swollen spherical, or nearly spherical stem, leaves are borne in a whorl and bear dormant buds in their axils. Prior to 1850 it was scarcely grown in Britain being then introduced from the Continent (Oldham, 1948). Smaller, tender forms are used for culinary purposes but larger, coarser types are sometimes grown for stock feed. Leaf development varies considerably, some of the quick growing cultivars producing only a very few small leaves. Not generally frost resistant, cold-hardy lines may be developed through selection (Krickl, 1944).

B. oleracea var. *italica* Plenck (sprouting broccoli)

Sprouting broccoli produces numerous heads of greenish or purplish flower buds used for culinary purposes. This variety should not be confused with the cauliflower (var. *botrytis* L.), the distinction is made by Helm (1960).

B. oleracea var. *botrytis* L. (cauliflower)

Contains all forms with tight, compact white heads or curds of anomalously developed floral organs. Its origin dates back to the sixth century B.C. (Boswell, 1949). There are winter forms (sometimes termed " broccoli " or " cauliflower-broccoli ") which are doubtfully hardy and quick maturing summer forms.

B. oleracea var. *acephala* D.C. (collards, tree kales, marrow stem kale)

This group appears to have its origin in the Mediterranean area or in Asia Minor about two thousand years ago. The best known form of this tall and unbranched variety is the marrow-stem kale, often grown as fodder for cattle. The characteristic swollen stem is high in sugar content. Plants are either cut and fed to stock, made into silage or grazed *in situ*. Most cultivars do not have a high degree of frost resistance and leaf development is generally rather poor. There is an indication that hardiness, palatability, uniformity and leaf retention may be improved through breeding (Thompson, 1959).

B. oleracea var. *fimbriata* Mill. (curly kale, dwarf scotch kale)

The curly kales are closely allied to thousand-headed kale but less branched and with intensely curled leaves. The high lamina to petiole ratio in the leaf may be important from the fodder point of view. Generally quite hardy curly kale is usually a culinary plant.

B. oleracea L. var. *fruticosa* Metz. (thousand-headed kale)

Kales have been in cultivation at least 2,000 years (Boswell, 1949). Thousand-headed kale, as the name implies, is a multi-headed type and branching low down produces numerous side-shoots. Commercial thousand-headed kale is generally fairly heterogeneous, especially variable is the degree of branching, some plants failing to produce side-shoots and resembling more the *acephala* forms. Other variable characters are the time of side-shoot development, length of petioles, size and shape of the leaves, etc. Only one truly distinct type has been developed. This form 'Canson' originated probably as a selection from ordinary thousand-head and is characterised by its lower growth and considerably higher leaf-stem ratio. The actual amount of leaf produced is, however, about the same as ordinary commercial thousand-head. Winter-hardiness and leaf retention of 'Canson' are good.

The value of autotetraploid B. campestris and B. oleracea

The autotetraploids of *B. campestris* and *B. oleracea* (which may be regarded as by-products in amphidiploid synthesis see method 2) may themselves be useful. This is especially so in fodder types where very high seed yield is not vital. The seed yield of newly produced autotetraploids is considerably lower than that of diploids (although individual seed weights may be greater) so that the value of 4x *B. campestris* as an oil-seed plant is somewhat limited. It is, however, possible to increase seed yield by selection over several generations.

Autotetraploid *B. campestris* ssp. *dichotoma* (toria) had 55·2 per cent heavier seed than diploids but produced an average of only 2·7 seeds per siliqua as compared with 13·8 seeds for diploids (Singh, 1958). Attempts to increase the fertility of 4x toria through the selection of single plants with high seed output was not effective. Parthasarthy and Rajan (1953) employed a mass pedigree system of selection consisting of the isolation of an elite population and the bulking of seeds of selected plants before sowing. Rajan

(1955) was able to raise the fertility of 4x *B. campestris* considerably by this method.

Svalöf's 'Sirius' turnip, a tetraploid derived from intercrossing three tetraploid strains of well known commercial diploids, was shown to outyield diploid cultivars in "root" production and in total dry matter but its protein content was slightly less. There was a suggestion that tetraploid turnips were more resistant to *Plasmodiophora*. Where well known commercial diploid turnips were compared with their autotetraploids the yield of tops was lower in 4x's in almost every case (Josefsson, 1955).

There is a suggestion that autotetraploid forms of *B. oleracea* may be economically useful and if the plants are to be used for fodder very high seed yields should not be vital. Biochemical differences associated with ploidy could be important. Barr and Newcomer (1943) analysed heads of equivalent size of a diploid cabbage cultivar and its autotetraploid. The 4x had 36 per cent more sugar, 33 per cent more colloidal nitrogen, 14 per cent less soluble nitrogen whilst the lower leaves contained 300 per cent more ascorbic acid. Autotetraploids of *B. oleracea* var. *gemmifera* (brussels sprouts) had fewer leaves than the diploid but the leaves were larger and broader. The tetraploid contained a higher number of small plants and showed greater mortality. There was little difference in dry matter content between 4x's and 2x's (Persson and Apeland. 1960). Similar results have been obtained by the author in diploid and tetraploid var. *fruticosa* (thousand-headed kale).

Cytology of autotetraploid B. campestris and B. oleracea

The possibility of obtaining a true and balanced amphidiploid as opposed to an aneuploid hybrid from crosses between autotetraploids obviously depends on the meiotic behaviour of the parents. In order for a stable amphidiploid ($2n = 38$) to be formed gametes containing 20 and 18 chromosomes respectively must come together. These will only result should meiosis in the autotetraploid species parents be regular.

Autotetraploid *B. campestris* ssp. *chinensis* was studied by Yakuwa (1944) who found univalents, trivalents and quadrivalents, apart from normal bivalents, at metaphase I of meiosis. Univalents and trivalents were rare but the quadrivalent frequency was 3·28 per cell (21 cells examined). In spite of these anomalies 64 per cent of the cells examined had balanced 20 : 20 plates at MII, suggesting that a fairly high number of gametes would contain balanced numbers of chromosomes. In *B. campestris* the author found a mean quadrivalent frequency of 1·33 for 58 cells. Only one trivalent was found. Of 139 cells examined at MII 78 (*i.e.* 56·1 per cent) showed regular 20 : 20 segregation, 57 cells 21 : 19, 3 cells 22 : 18 whilst in one cell 23 : 17 segregation was seen. Pollen fertility was around 95 per cent.

Howard (1939) studied chromosome pairing in autotetraploid kale (*B. oleracea* var. *acephala*) and found a mean quadrivalent frequency of 4 per cell. At anaphase I 18 : 18 segregation was common and 57 per cent of MII plates contained 18 chromosomes. Chromosome pairing in newly produced autotetraploid *B. oleracea* var. *fruticosa* was studied by the author who found a mean quadrivalent frequency of 1·5 per cell, univalent frequency was 0·46 whilst there were only two trivalents in 152 cells. Of 287 cells examined at metaphase II 212 (*i.e.* 73·9 per cent) showed completely regular 18 : 18 segregation.

The chromosome behaviour of both 4x *B. campestris* and 4x *B. oleracea* is such that a high frequency of gametes containing balanced numbers of chromosomes is to be expected. In spite of this some aneuploids may be anticipated amongst the progeny, the author has found plants with 2n = 37, 2n = 35 and 2n = 34 in C1 autotetraploid *B. oleracea*. Most plants were balanced euploids (2n = 36). The presence of aneuploids in the early generations of colchicine-induced autotetraploids should be little handicap towards increasing seed fertility, selection for good growth characters and general fertility might eliminate, or at least greatly reduce, their presence in later generations.

Barriers to hybridization between B. campestris and B. oleracea

Environmental conditions at the time of pollination may profoundly influence the success or failure of a particular cross. Hosoda (1961) found that better fertilisation in crosses between *Brassica* species was obtained at relatively low temperatures and there is no doubt that humidity is another important factor, a fairly humid atmosphere being desirable. The state and age of the pollen is obviously important, fresh pollen (*i.e.* pollen from newly dehisced anthers) should be used whenever possible. *Brassica* pollen loses its viability fairly rapidly under normal greenhouse conditions and after two days viability is almost nil (as determined by pollen germination experiments in the laboratory).

Pollen of almost any *Brassica* species seems capable of germinating on the stigma of any other species but in the cross *B. campestris* × *B. oleracea* and its reciprocal it has been shown that, although penetration of the stigma may take place, coiling of the pollen-tubes occurs within the style (Röbbelen, 1960) so that many pollen-tubes may be unable to reach the embryo sacs in time to effect fertilisation; to a certain extent this may be overcome by pollinating in the bud stage, *i.e.* two or three days before normal opening of the flower. It is also possible that stylar incompatibility may be overcome or by-passed by intra-ovarian injection of pollen as suggested by the work of Maheshwari and Kanta (1961) in other genera. Fertilisation of excised ovules *in vitro*, achieved in *Papaver somniferum* by Kanta *et al* (1962), is an interesting technique which might be applied to *Brassica*. Davies and Wall (1960) have shown that gamma irradiation of pollen or female plants before crossing may slightly increase the chances of obtaining hybrids in some interspecific combinations within *Brassica*.

Apart from the incompatibility within the style embryo abortion may result from endosperm deficiency after fertilization has taken place (Håkansson, 1956). This suggests that hybrids might be raised by excising the embryos and growing them *in vitro*. A suitable technique has been devised for brassicas by Nishi *et al* (1959).

It is theoretically possible to produce synthetic *B. napus* from any combination of *B. oleracea* and *B. campestris sensu lato*. Because *B. napus* is a true amphidiploid and its chromosome pairing is entirely autosyndetic it is not possible to predict accurately the appearance or performance of any synthesised form and the potential variability of any synthetic is somewhat limited. It will be seen that from an examination of the variation within both *B. campestris* and *B. oleracea* that there is adequate material available which may be combined to form new and true breeding amphidiploids which may be of benefit to agriculture. One of the greatest difficulties lies in obtaining hybrids in any number, but recent work with auxins, grafting and embryo excision, etc., suggests that barriers between the species may be broken down and new forms more readily synthesised.

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BIOSYSTEMATICS AND CLASSIFICATION

V. H. Heywood
The Hartley Botanical Laboratories,
University of Liverpool

With the recent establishment of the International Organization of Biosystematists, a further step has been taken towards the recognition of a separation between some, at least, of the aims and activities of orthodox systematists and experimental systematists. The different spheres of activity of the two have never been fully clarified, and it is in the very nature of the problem that a degree of overlap between them will continue to make this difficult. This topic was debated at some length by several speakers at a recent symposium on biosystematics at Montreal (see Heywood & Löve, 1963).

Certainly during the past few years the relative roles of orthodox and experimental taxonomy (biosystematics) have become much clearer. These may be briefly summarized as follows: *Orthodox taxonomy* aims to provide a reference system and is based primarily on correlations of phenetic attributes. Its basic classificatory unit is the species which is treated as a group of individuals possessing attributes in common and recognizable by easily perceptible criteria, and is separated from other such groups by discontinuities in correlated features. These species are grouped into higher taxa on the basis of common resemblances. *Biosystematics* appears to cover at least two kinds of aim: the first is to extend our knowledge of species and other taxa as they exist as natural populations in the field. This includes knowledge of their breeding behaviour, chromosome numbers, genetics, ecology, etc., and represents an extension of orthodox taxonomy and is inseparable from it. The second kind of activity embraced by biosystematics is a study of what might be termed evolutionary dynamics and does not have as its primary aim the classification of the resultant information into formal categories. It embraces much of genecology, parts of population genetics, experimental morphology and similar fields.

What is not so clear is the relationship that exists or should exist between these separate approaches to the study of variation. Some of the questions that must be asked are, what is the role of the orthodox classificatory system in experimental work, how useful are its categories for dealing with population variation, what relationship is there between orthodox classification and attempts to systematize genecological and other kinds of population variation?

The role of the taxonomic species and infraspecific taxa in relationship to population studies is widely misunderstood. For example, there is a widespread assumption that when defined in terms of phenetic attributes as opposed to gene-pools the species has little " biological " value. Also, it is not fully realized that in practical systematics the species category is still today overwhelmingly used in a pragmatic sense, so that individual species are morphologically recognizable, even in the face of experimental evidence which would allow more specialized and limited definitions (for example, restrictions of gene-exchange) to be employed. Although it is very evident that our knowledge of many named taxonomic species allows us to consider them in terms of breeding populations, it is not the adoption of any particular definition or philosophy that has permitted this, but simply our increased knowledge of the originally defined morphological units. To put this more precisely, the orthodox taxonomic species remains, in the vast majority of cases, the starting off point of our knowledge and it is important that this should be acknowledged as an act of deliberate policy. It is the common denominator.

The criticism of taxonomic species on the count of their lack of " biological " validity results from a failure to distinguish between a number of different aspects, such as the definition of the species as a taxon, the evidence used to satisfy this definition, the evidence used to recognize the species and information acquired later.

Taxonomic species are defined in terms of character correlations (overall similarity, still in most cases assessed visually by the taxonomist) shown by their members, and correlated discontinuities in the variation pattern of two or more attributes. These discontinuities when very high (up to 100 per cent) are termed *diagnostic* characters; those which are not so high (say, 70-80 per cent) are often called *differential* characters. The *total* evidence used to arrive at a decision regarding specific distinction may come from many fields—anatomical, cytological, physiological, embryological as well as morphological—

but that part of it used to *recognize* the species is, for practical purposes, easily perceived and in the case of Angiosperms morphological. Recognition of species by apparently trivial characters such as leaf shape, flower number, etc., are reflections of the principle of correlations and in no way conflict with the use of a great deal more evidence in satisfying the definition of the species. It may be helpful to regard these diagnostic characters as markers, if we can borrow from the jargon of genetics—marking off discontinuous groups, the emphasis being on *groups*, implying character correlations. Likewise it must be remembered that only a small part of the evidence is presented in the *descriptions* of taxa, the description being an abstract for the convenience of the user (Davis & Heywood, 1963).

Species may be proposed on the basis of minimal evidence—a few randomly collected specimens which, on the basis of clearly visible morphological attributes, form a distinct but separable group in the herbarium. Countless species have been described on such an unsophisticated basis. From a legalistic point of view such species are legitimate if duly published in conformity with the current nomenclatural code. The " biological " validity of such species, *i.e.*, of the population unit that can be extrapolated from the original description, may not be confirmed for many years or even decades (if at all) until more material has been collected and the proposed unit shown to represent a natural population. This leads on to a critical point—does the taxonomic species comprise a group of interbreeding individuals? The answer is twofold. The definition of the species as a taxon implies nothing about its breeding relationships; *individual* species, however, may or may not represent such intrabreeding groups. Perhaps the majority of well-known species do, although the proportion they constitute of the total number described is probably much smaller than is generally assumed. We should be quite clear on this: taxonomic species are not, by definition, intrabreeding groups, or indeed populations at all in any but the loosest sense of the term; and although many species are undoubtedly biological in the modern sense, this cannot be automatically assumed for all species. From this it follows that users of taxonomy must treat each species on its merit. This conclusion has, of course, proved unpalatable to many recent biologists who have proposed restricting the use of the term species to reproductively isolated Mendelian populations. This is not the place, however, to discuss the consequences of such moves: for one thing they would simply cause a semantic problem by necessitating another term for the majority of species about which this is not true; and for another there is no agreement as to the criteria by which such full biological status would be adjudged.

Even in well-studied species which have been collected and observed in the field thousands of times and which can be safely regarded as forming natural populations of ostensibly interbreeding individuals, there are many reasons why interfertility of all members cannot be assumed. Intraspecific polyploidy may occur, forming a highly effective breeding barrier between individuals at the different polyploid levels; chromosomal rearrangements or genic alterations may cause similar effects; members from widely separated parts of a species population or population series may show reduced fertility or even intersterility; or the breeding system may be different.

Consequently taxonomic species may comprise one or more gene-pools within a single morphological framework and in evolutionary terms represent different situations.

The role occupied by the *subspecies* is an interesting one. Although there are, of course, exceptions the commonest usage of the subspecies category is for major geographical segments of taxonomic species. Subspecies in this sense are normally separable from each other by fairly high discontinuities in a number of features but show no absolute correlated discontinuities in the variation pattern (*cf.* Hedberg, 1957). In practice this comes to mean that not all individuals can necessarily be identified with one or other of the subspecies unless evidence as to provenance is available, although about 75 per cent of them can (the 75 per cent rule which serves as a guide although not strictly adhered to). It should be pointed out that subspecies can only be recognized meaningfully after a species has become quite well known as a variable population. It is therefore largely a population term and agrees broadly with the genetic concept of races as open-ended systems of populations between which gene-exchange occurs. Subspecies, when they meet, tend to intergrade—presumably as a result of gene-exchange although this has of course to be demonstrated. Not all intermediates between subspecies need be interpreted in this way: in some cases two species have not been clearly delimited in the past and the intermediates may be the result of failure to appreciate the species' limits; or, in other cases, the subspecific pattern of variation may be the result of the meeting of previously separated species populations.

Below the rank of species taxonomists often recognise varieties and forms, but apart from the usage of the variety in the sense of a micro-subspecies little is gained by their use except in a purely formal sense.

The conclusions that might well be drawn from these considerations is that the species-subspecies-variety hierarchy can be used to describe population structure. This has been contested by Mayr (1959) because of the following features of geographical variation which render the non-arbitrary definition of subspecies difficult:

(1) Tendency of different characters to vary independently geographically.
(2) The independent recurrence of taxonomically similar populations in widely separated areas (polytopism).
(3) The occurrence of microgeographic races (micro-subspecies).
(4) Arbitrariness of the amount of differentiation selected by different authors to justify the recognition of slightly local populations.

Acceptance of these difficulties does not invalidate the usefulness of the subspecies. Although the subspecies necessarily conceals much of the detail of variability both within and between populations, Mayr is correct in stressing that it is this very oversimplification that makes it so valuable in classification. This is equally true of the species and it is one of the most important aspects of the orthodox system of formal classification. The moment we attempt to make our taxa too precise by introducing non-arbitrary criteria, or ones that cannot be simply and generally applied, we destroy the general utility of the system.

In summary, the taxonomic species and subspecies can deal adequately with variation for the purposes of general classification—the record shows this amply enough. But clearly the experimentalist, the genecologist, the population geneticist, etc., wants not only a reference framework at a gross level but is intimately concerned with population variation at a level at which taxonomic recognition is not possible or of a kind which is not susceptible to categorization or fitting into variational units at all.

For the experimentalist, in particular the genecologist, there are two main questions to be considered. Firstly, what variational phenomena does he wish to record? Secondly, do any of them need to be described and named and if so for what purpose? The restrictiveness of the genecological system of Turesson is now widely recognized (Gregor, 1963) and although some ecotypes coincide sufficiently well with taxonomically recognizable units (varieties or subspecies) to be named formally (Heywood, 1959) they are sufficient of an exception as not to affect the main issue.

Böcher (1963) has drawn attention to some of the kinds of biological information of importance that cannot be reflected in formal taxonomy, for example, variation in life-form, habit, etc., in different parts of a species area. In these, and other similar cases, the ad hoc *deme* terminology would seem to be admirably suited (Gilmour & Gregor, 1939; Gilmour & Heslop-Harrison, 1954; Gilmour, 1960).

When applied to ecotypic situations the *deme* terminology may be employed as suggested by Gregor (1963). Thus individual investigators would record such genoecodemes, for example, as they wished in a particular species and these could be recorded in Floras by listing the categories to which the examples had been assigned under their respective taxa, adding references to the literature where the relevant details are recorded, *e.g.* under *Plantago lanceolata*: genoecodeme (Gregor & Watson, 1961). The *deme* terminology is deliberately not designed for formal communication, but it is likely to have to serve a much greater role in communication when more examples of similar *demes* are recorded. Up to the present the system has been little used outside Britain, and furthermore the number of ecotypes (genoecodemes, etc.) recorded has been comparatively few. With the more widespread adoption of the system and the continued description of further examples it is inevitable that some more formal method of recording and distinguishing between them will be needed, and in the light of similarities or parallels between others of them, there will be a need for some kind of informal hierarchization. For communication and meaningful interpretation of results systematization of knowledge is necessary.

It may well be found in the future that a whole series of similar genoecodemes with similar phenotypic characteristics have been recorded within a species by different authors in different countries. Countless situations of this nature will arise. The need for international registration of ecodemes and for a means of distinguishing between them and of ascertaining which, if any, are " the same " might well have to be considered. We are only just beginning to see what kinds of problems of classification and communication may lie ahead. One thing is clear, the orthodox classificatory system will come to play an increasingly important role as more and more kinds of information are attached to its framework.

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A REVISION OF THE TUBER-BEARING SOLANUMS

(Second Edition)

J. G. Hawkes
Department of Botany, University of Birmingham

Since the publication of the first edition of this Revision in 1956, several important works on the taxonomy of wild and cultivated potatoes have appeared. New species have been described by Vargas (1956) and by Ochoa (1956-62) from Peru, and by Cárdenas (1956) from Bolivia. Bukasov (1959) has given some new opinions on the classification of the tuber-bearing species and commented on previous work ; and Correll (1962) has published a comprehensive monographic treatment of the potato and its wild relatives. This latter work gives good descriptions and drawings of all species known up to the time of publication and includes a considerable number of species, varieties and forms described by the same author in 1958 and 1961. A study of the biology and relationships of the wild and cultivated potatoes of Argentina and adjacent countries is being prepared by J. P. Hjerting and the present author, and is due for publication shortly. Some new species and nomenclatural changes have been published as a result of this work, also (Hawkes & Hjerting, 1960). Apart from these more strictly taxonomic works much new information is now available on species relationships, derived from cytological, genetical, comparative biochemical and serological work. The results of recent collecting expeditions have told us more about species distribution, ecological adaptation and the genetic basis of disease resistance. I am very much indebted, therefore, to Dr J. W. Gregor, Director of the Scottish Plant Breeding Station, for kindly affording me the opportunity of publishing a second edition of this Revision.

The present work attempts, as did the first edition, to give a clear conspectus or general classification of all the tuber-bearing *Solanum* species known up to the date of publication. Unfortunately it has not been possible to include dichotomous keys for the identification of all species, because of the enormous increase of newly described species that are insufficiently known at present. Nevertheless, it is hoped that the potato breeder will be able to verify the identity of most of the material on which he is working and will be able also to view his material in relation to the totality of potato species now known.

In the present work, as before, I have tried to present a classification in accord with modern cytogenetical views of potato species. Although in the first edition I was able to reduce almost half the known species to synonyms, an additional 63 species have now been described ; and since, because of their recent publication, I have no knowledge of most of these in the living state, it has not been possible, in most cases to do more than indicate their probable affinities.

In addition to the keys, I have also included short descriptions of the species now recognized, together with their synonyms[1] and references to the sources of the original descriptions. In a work of this length there is unfortunately not space enough to discuss the detailed taxonomy, phylogeny, cytology, breeding behaviour or disease resistance of each species, but this is being prepared in detail for later publication in book form. In the present edition I have given details of subspecific classification, since much more is known of the infra-specific variability of potato species than was the case in 1956. I have also noted natural distribution, habitat, altitude range and chromosome number for each species and subspecies where these are known.

In the main, then, this paper is a summary of the revised classification of potato species which is being prepared by the present author, and it is hoped that it may be of some value to plant breeders, cytologists and geneticists in this field.

The species concept in Solanum

The German taxonomist Bitter, working almost exclusively on dried herbarium material, thought of *Solanum* species as very narrow units with little infra-specific variability. Even the slightest variants were given specific, sub-specific or

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[1] The synonyms are confined to those described as species or subspecies. For reasons of space I have not included all the varietal or form synonyms, but the reader may assume that these are to be considered as synonyms unless otherwise stated.

varietal rank, and his species were generally based on only one or at most a very few specimens. The Russian botanists and plant breeders, notably Juzepczuk and Bukasov, followed Bitter's methods fairly closely, basing their descriptions for the most part on living material. Thus any collection that was found to differ significantly from the descriptions of Bitter or other taxonomists was described as a new species, variety or form. Their most important contribution to this field was undoubtedly the discovery of a polyploid series of species within the cultivated potatoes of South America and the stress they laid on the value of wild and primitive cultivated forms to the plant breeder (Rybin, 1930 ; Bukasov, 1933, etc.).

The present writer, working during the war on the collections of potatoes brought back by the Empire Potato Collecting Expedition and without a complete range of type specimens available, continued with the taxonomic methods of Bitter, Juzepczuk and Bukasov until 1945. It was then decided to begin a revision of the whole subsection *Hyperbasarthrum*, and for this purpose many thousands of herbarium specimens were obtained on loan from herbaria in Europe and the Americas.

It became evident after a year or two that our concept of the species in *Solanum* must be very drastically revised if we were not to arrive at a state where nearly every new collection of material was given a distinct specific or varietal name. Even from herbarium studies it was possible to see that the species must be regarded as larger units, comprising a rather wide range of infraspecific variability ; this variability could rarely be fitted into the conventional pattern of varieties and forms, though geographical variation enabled one to see that subspecific divisions were often both useful and necessary.

Before attempting to publish a revision of this group based on herbarium studies it was considered of vital importance to verify as many as possible of these conclusions by experimentation. Hybridizations between species or putative species, taken in most cases to the F_2 generation, have given results agreeing on the whole with the concept of larger specific units in *Solanum*. The details of this work are being prepared for publication later.

The classification given in the present work differs in several respects from that of Correll in his recent monograph, due mainly to the fact that I have tried to take experimental results into consideration when fixing species boundaries, and have regarded potato species as being at once highly variable genotypically and of extreme phenotypic plasticity. Correll, indeed, also calls attention in his earlier work (1952) to the variation of phenotype to be seen in species such as *S. demissum*, *S. verrucosum* and *S. stoloniferum*, when growing in natural conditions, in the experimental field or in the glasshouse ; he points to the very real difficulties that arise when type specimens are taken from material cultivated in field or glasshouse for some species and from plants collected in the wild for other species. On the whole, however, and especially in his more recent monograph, he seems to have relied chiefly on the well-tried classical taxonomic method of grouping plants together by means of maximum correlation of characters. This method would be reasonable enough in a group with very little phenotypic plasticity, or where each species grew in a reasonably constant natural environment, or if it were possible to grow every collection under known and fairly uniform conditions so as to eliminate the variation factor caused by differences of habitat.

Clearly, none of these three possibilities fits the situation as we know it in *Solanum*. Phenotypic plasticity within most species is very great ; environmental differences in nature are such as to cause great phenotypic differences ; and one cannot hope to grow every collection of *Solanum* in the experimental field, since our herbaria are full of specimens for which no seed or tuber collections were made ; and all these collections need to be identified. What one can hope to do is to arrive at a compromise solution to the problem by trying to cultivate at least *some* accessions of most species under uniform experimental conditions and to compare these phenotypes with those of the identical genotypes growing under natural conditions. This involves detailed collections by persons well-versed in the taxonomic and genetical implications of the operations in which they are engaged, together with careful follow-up work in the glasshouse and experimental field. It then becomes possible gradually to build up an idea of the range of phenotypic variation of a given species under the widely varying environmental conditions encountered by it in nature and to contrast this with the phenotypic ranges of closely allied species.

When this is done (and it has admittedly been accomplished so far with only a limited number of species) we can see that in some cases two apparently distinct species, as judged from the type specimens gathered in the wild, are one and the same entity—that their apparent distinctness was due to widely varying habitat and no more. In other examples the phenotypic variation *in nature* is so intense as to obscure almost completely the expression of the essential genotypic characters that point to the differences between species. We can then begin to understand that certain characters are of little taxonomic value, in that they vary in a parallel manner in two or more species according to environmental changes; the "essential" characters that are of value in delimiting the species can very easily be overlooked under such circumstances until we have become really familiar with the pattern of variation of the species we are studying under known and varying environmental conditions.

It is therefore essential whenever possible to grow accessions of species from varying habitats under experimental conditions, in order to elucidate the essential and valid taxonomic characters. This of course takes time, and has been accomplished for only a very small proportion of the total number of species. The present writer has been able to grow much more material of species from Argentina, Uruguay, Brazil, Mexico and Central America than has been possible of species from Peru and Bolivia. These latter countries are still largely unknown from the experimental point of view, though much valuable work is now being carried out in Bolivia by Cárdenas and in Peru by Ochoa.

Most tuber-bearing *Solanum* species, at any rate at the diploid level, seem to be kept apart largely by eco-geographical boundaries; in some instances genetical and crossability barriers seem to function, but they are seldom complete. Thus the group of species as a whole is of particular value to the plant breeder in that transference of genes from most species to *Solanum tuberosum* can probably be effected, given the time, patience and technical knowledge.

Probably F_1 hybrids are formed with some frequency in nature between most species whose distribution areas overlap; but it is also probable that under completely natural conditions these hybrids will not be able to survive because their gene combinations are not fitted to the "adaptive peaks" of their parents. Thus F_2 segregates or backcross segregates will not normally be formed. However, this completely natural situation has in many areas long since ceased to occur, since the whole ecological balance has been changed by the advent of man. No doubt rather slowly in pre-conquest days and much more rapidly in recent historical times, man has proceeded to alter and destroy the natural plant communities by his agricultural and other activities, so producing many intermediate habitats where hybrids between species can now exist and reproduce. We know of at least one case, and suspect the presence of a number of others, where the boundaries between species that were once presumably sharp and clear-cut, are now becoming obscured; in the best authenticated instance (that of *S. chacoense* and *S. microdontum*) the species concerned possess rather sharply contrasted characters, so that it is relatively easy to detect the process of introgressive hybridization between them. Where the species are not so distinct or where they are not sufficiently well-known, the very process of introgressive hybridization may be obscuring their boundaries and rendering it more difficult for us to understand their variation pattern. Furthermore, in regions of ancient civilization, such as the central Andes of south Peru and north Bolivia, the destruction of natural habitats must have taken place in the more distant past, thus allowing time for introgression to have progressed to such a point that possibly the original species may now have completely lost their former identities. It is interesting to note that it is precisely in central to south Peru and north Bolivia where the biggest taxonomic problems are to be encountered.

In view of what has just been said it will be seen that some species, in general those from the southern and northern ends of the distribution area of the group, are better known than others, and that this second edition of the Revision will of necessity be somewhat uneven in treatment. On the whole, most of the better-known species seem to possess a rather wide geographical distribution and to be split up into a number of geographical subspecies, linked together by intermediate forms; these subspecies within each species show great similarities of habit and ecological preference.

Where species are not so well known, then in many, and perhaps most, cases the subspecies or even phenotypic variants have been described as distinct species. As my knowledge of them has increased, I have been able to link these "species" together as taxonomic synonyms or as geographic subspecies. The classificatory schemes put forward by Bukasov, Correll and others do not generally include subspecies of this type. These authors either upgrade the entities classed by me as subspecies into distinct species (sometimes, indeed, in distinct series) or downgrade them to varieties or forms. In my own view, it is useless, and indeed misleading, to attempt to describe the variation within *Solanum* species by dividing them into varieties of forms, and I have relegated all these to synonymity under the appropriate species or subspecies.

Where I have been able to examine material of the new species described by Correll, Ochoa, Cárdenas, or other authors, even if it was in the form of dried herbarium specimens, I have in many cases made a decision as to whether these species should be regarded as distinct or as synonyms of previously described ones. Where I have seen no material I have retained the species as such, and have noted this fact, together with my views on their possible affinities.

I have been rather conservative in my attitude to the number of series or groups of species, since it seems to me that excessive splitting of series defeats the ends for which they were created, namely, to help us group species together for ease of identification and memorization. Nevertheless, it must be admitted that the series are also to some extent "natural", in that, by describing them we are trying to group together species with fairly recent common ancestry, so that we may show their evolutionary relationships. Unfortunately, we know practically nothing about the evolutionary relationships of many of the series proposed for South American species, and I have therefore thought it wiser to make as few changes as possible in this new edition.

The pattern of variability in the tuber-bearing *Solanum* species cannot be adequately understood without a realization of the importance of the two alternative means of reproduction available to them—sexual and vegetative. Although our domestic potato, *S. tuberosum*, commonly reproduces vegetatively the reverse is largely true for the wild diploid and even-numbered polyploid species. Even amongst the South American cultivated diploid and tetraploid species sexual reproduction probably plays a more important role than has hitherto been admitted.

In view of the fact that the majority of wild potatoes cannot maintain themselves in competition with natural climax or even sub-climax (grassland) vegetation they tend to colonize bare or disturbed soil for rather short periods and are ousted when the natural vegetation once more returns. Under such conditions reproduction by tubers is therefore of only limited utility. A number of species, however, are able to grow more or less indefinitely in open semi-desert, scrub, rocks, cliffs and screes and in very stony ground where conditions are too dry or inclement for the normal plant cover to be complete. From this it follows that potato species will naturally colonize many areas where the natural vegetation is kept in check by man or his domestic animals.

Such species, therefore, that are able to grow on these "open" situations for long periods will not only be able to adapt themselves to changing environments by means of natural selection operating on a very large number of genotypes produced by sexual reproduction; but they will be able also to maintain themselves almost indefinitely by means of clonal propagation (depending on the conditions noted above) when a particularly successful genotype has established itself. This combination of the "best of two worlds" may perhaps be compared with the process of facultative apomixis in certain other plant genera.

The position of the odd-numbered polyploids (triploids and pentaploids) is also worth examining at this point. These are maintained entirely by vegetative propagation since they are either highly sterile or, if relatively fertile, cannot breed true because of their unbalanced chromosome sets. These "species" are either the result of diploid × tetraploid crosses or are sterile auto-triploid forms of normally fertile diploids. They are chiefly to be found wild in the environs of large cities where the disturbance of the natural vegetation enables them to grow vegetatively under the protection of man for perhaps indefinite periods of time. Examples of such triploid forms are seen near Mexico City (*S. bulbocastanum*, *S. cardiophyllum*); Lima, Peru (*S. medians*); Valparaiso, Chile (*S. maglia*) and Montevideo, Uruguay (*S. commersonii*). Cultivated hybrid species are of course also maintained directly by man and reproduce wholly vegetatively.

Such sterile hybridogenic species are obviously quite distinct, both in their formation and reproduction, from the sexually fertile ones, and the advisability of giving them specific names may be questioned. We include them here chiefly for convenience and also because a number of them are very widespread and are continually being collected and worked on by plant breeders.

In the sexually reproducing diploids and in most of the tetraploids and hexaploids allogamy is the dominant breeding system. Most of the diploid species (with the exception of *S. brevidens, S. etuberosum, S. morelliforme* and *S. verrucosum*) are self-incompatible, the mechanism involved being generally assumed to be of a simple oppositional factor type. This outbreeding system ensures that gene flow shall take place through large populations, and seems to have been responsible for maintaining the high degree of infraspecific variability which we have already commented on.

Although the tetraploid and hexaploid species are self-compatible most seem to require an insect pollinizing agent before seed can be set, due probably to the difference in position of the anther pores and the stigmatic surface. No data exist, however, as to the extent of self-pollination under natural conditions, though certainly very little occurs on plants grown in insect-proof glasshouses. Species such as the hexaploid *S. demissum* and the tetraploid *S. acaule* are normally self-fertilized, probably due to the short style and consequent proximity of stigma and anther pores ; however, these two species are noteworthy exceptions to the general rule of obligatory or facultative out-pollination in the group.

Another problem in the tuber-bearing *Solanums*, which has already been referred to, is the frequent occurrence of natural hybridization in the areas where two species overlap in their geographical or altitudinal ranges. In view of the absence or incomplete functioning of sterility barriers (the majority of the species being kept apart largely by means of eco-geographical or altitudinal barriers) and the weakly expressed genomic differentiation in the sub-section, this natural hybridization is not surprising. Nevertheless, in spite of hybridization many, though possibly not all, the species are able to maintain themselves as distinct entities.

The presence of a large percentage of weak and unthrifty individuals in F_2 progenies of species crosses, due to their possession of disharmonious gene combinations from the two parents, may be of importance in *Solanum* for keeping the species distinct in nature. Progenies of this sort raised by the writer at Cambridge and at Birmingham have thrown considerable light on species relationships. It seems probable, on the other hand, that the lack of unthriftiness in F_2 progenies may not necessarily mean that the taxa under test are conspecific. They may possibly have evolved for some period in spatial isolation, the breeding barrier in this case being eco-geographical or altitudinal, and not genetical. In circumstances such as this a very thorough taxonomic analysis of the characters of the species under review is necessary to augment the experimental data and to demonstrate whether any considerable overlap of characters between the two species can be detected.

Subdivisions of the genus Solanum

The genus *Solanum* L., to which the wild and cultivated potatoes belong, is extremely large, containing over 2,000 species. Most are herbs or small shrubs, often clothed with thorns, and in fact less than one-tenth of the genus is tuber-bearing.

Dunal (in de Candolle, 1852) who was the first specialist in the genus, divided it into two sections, *Pachystemonum* and *Leptostemonum*. The former section included plants with thick anthers and no thorns, whilst the latter contained species with long narrow anthers and stems and leaves often provided with thorns.

The tuber-bearing species are included within *Pachystemonum,* which Dunal further subdivided into 5 subsections. Of these, only the first, *Tuberarium,* need concern us here, since it contains the potatoes and related species. They are distinguished by actinomorphic flowers, a jointed or articulated pedicel and generally imparipinnate leaves. Recently Correll (1962) has described the section *Neolycopersicon,* which seems to form an evolutionary link between the rest of *Solanum* and the genus *Lycopersicon*. The species *Solanum pennellii* has been placed in this section and can be hybridized both with *Lycopersicon* on the one hand and species in section *Tuberarium* on the other.

Bitter (1912, *et seq.*), who made perhaps the most extensive contribution to our knowledge of the genus, elevated sections *Pachystemonum* and *Leptostemonum* to the rank of subgenera, the former subsections (including *Tuberarium*) then being regarded as sections. He also divided *Tuberarium* into two subsections, namely :—

1. *Basarthrum.*—Pedicel articulation at the base; no stolons or tubers; plant provided with 2-celled bayonet-hairs. None of these species has been crossed with species in the following sub-section.

2. *Hyperbasarthrum.*—Pedicel articulation situated at least some distance above the base. It may be very low in some species (series *Etuberosa*), but in any case the two-celled "bayonet hairs" are never found in this subsection. On the other hand the articulation is often placed very high up, just below the calyx base. Although most species in *Hyperbasarthrum* are tuber-bearing, a few apparently do not possess stolons or tubers (Series *Juglandifolia* and *Etuberosa*); nevertheless they are placed here because of their general morphological similarities to the tuber-bearing species.

Subsection *Hyperbasarthrum* was further subdivided into groups or series by various authors. In the present work seventeen of these series are recognised, though it is considered possible that further divisions of series *Tuberosa* may be necessary when certain of the wild species in this series become better known.

The detailed taxonomy of subsection Hyperbasarthrum

In the treatment of *Solanum* species given in the following pages the species are arranged under their appropriate series in the following manner :—

(i) Species known in the living state are listed alphabetically.

(ii) Species known only in the form of herbarium material are presented in smaller type directly following group (i) in each series and are also arranged alphabetically.[1]

(iii) Species whose identity is doubtful or ambiguous and others whose names have been mentioned in the literature without an adequate description (*nomina nuda*) are listed in an Appendix on p. 160.

[1] See also Appendix IV, p. 172.

In addition I have included for easy reference a table (p. 165) of those species that have been studied in the living state, arranged according to taxonomic series and chromosome number, with notes on the country or countries to which each species is native.

It should be noted that the artificial keys for identification may lead to incorrect results at times owing to the ability of potato species to assume very different growth forms under different environmental conditions. Thus material grown under glass or under extremes of moisture or drought, or specimens attacked by viruses and other diseases probably will not be typical and will therefore be hard to identify. There are probably also a number of weaknesses in the keys themselves which only experience will uncover. It is therefore essential that when material has been "keyed out" it should be checked against the descriptions given in the text, and if discrepancies arise the key should be followed through again as carefully as possible to discover the source of error.

Unfortunately space does not permit the inclusion of an illustrated glossary explaining the descriptive terms used here, but these may be looked up in any good dictionary of botanical terms or in the glossaries that are given with most floras.

Key to series within subsection Hyperbasarthrum

1. Flowers bright yellow; stem generally woody; no stolons or tubers . . . . . **I Juglandifolia** (p. 90)
   Flowers white, cream, purple, pink, &c.; stem ± herbaceous 2
2. Pedicel articulation situated at or very near base (0-4 mm.); no stolons or tubers; berries round **II Etuberosa** (p. 92)
   Plant without the above combination of characters . 3
3. Corolla stellate, its lobes as long as or longer than broad, not sharply delimited from acumen 4
   Corolla rotate, pentagonal or sub-stellate, the lobes as broad or broader than long, generally well delimited from acumens 13
4. Berries long conical or ovate-conical, more than $1\frac{1}{2}$ times as long as broad 5
   Berries round or very slightly oval, less than $1\frac{1}{2}$ times as long as broad 8

5\. Plant with very wide often subcordate terminal leaflets; laterals greatly reduced or absent; flower white, less than 1·5 cm. in diameter . **VII Circaeifolia** (p. 106)

Plant without a great size difference between terminal and lateral leaflets 6

6\. Plants with white flowers and soft pubescence (Mexico) **V Pinnatisecta** (in part) (p. 96)

Plant with mauve flowers, glabrous or with coarse hairs 7

7\. Plants with acuminate, not decurrent leaflets **VIII Conicibaccata** (in part) (p. 107)

Plants with obtuse or rounded decurrent leaflets **VI Commersoniana** (in part) (p. 101)

8\. Flowers very small, not more than 1·5 cm. diam.; anthers narrow, somewhat adhering to each other laterally; plant generally epiphytic **III Morelliformia** (p. 94)

Flowers more than 1 cm. diam.; anthers ± ovate-lanceolate, free; plants terrestrial 9

9\. Corolla lobes narrow, more than twice as long as broad, or if shorter, deep cream in colour 10

Corolla lobes broad, less than twice as long as broad, never deep cream in colour 12

10\. Leaves simple; plant generally rather pubescent **IV Bulbocastana** (p. 94)

Leaves pinnate or pinnatisect; pubescence sparse or absent 11

11\. Leaflets long and slender, with rounded or oblique base; stigma clavate to capitate (Bolivia). (*S. yungasense Commersoniana*) (p. 106)

Leaflets with cordate to decurrent base, short, ovate to lanceolate; stigma saddle-shaped (Mexico) **V Pinnatisecta** (in part) (p. 96)

12\. Leaflets sessile, decurrent (Mexico, C. America) **V Pinnatisecta** (in part) (p. 96)

Leaflets petiolulate, not or only slightly decurrent **VI Commersoniana** (in part) (p. 101)

13\. Berries long conical or ovate-conical, more than 1½ times as long as broad 14

Berries round or only slightly oval, less than 1½ times as long as broad 16

14\. Corolla white; plant with dense pubescence of long simple hairs and short stalked glands **XIII Polyadenia** (in part) (p. 125)

Corolla blue to purple; plant without dense glandular pubescence 15

15. Corolla lobes very short and with small acumens, giving the flower a ten-lobed appearance; filaments quite glabrous (Mexico) . **XI Demissa** (in part) (p. 117)

Corolla lobes of medium length, with well-developed acumen, or if short, then filaments with well-marked pubescence (Mexico to S. America) **VIII Conicibaccata** (in part) (p. 107)

16. Berries ovoid, with flattened apex; leaves shining, glabrescent, marginally revolute when dry; stem glabrous, or if pubescent, then with long weak spreading hairs . . . . . . **X Piurana** (p. 111)

Plants without the above combination of characters . 17

17. Corolla with very short lobes and small acumens; lobes roughly equal in length to acumens 18

Corolla without such short lobes, rotate, pentagonal or substellate 20

18. Cultivated plants with pigmented tubers and stolons, generally tall-growing **XVII Tuberosa** (in part) (p. 154)

Wild plants, generally low-growing, with unpigmented tubers and stolons, or pigment only flushed over tuber, never in definite patterns 19

19. Rosette plants with the acroscopic basal lobe of each lateral leaflet better developed than the basiscopic lobe; articulation of pedicel very high up, well marked or represented only by a ring of pigment or entirely absent **XI Acaulia** (p. 116)

Plants sometimes in a rosette, often tall growing, the acroscopic basal lobe of each lateral leaflet not so well developed as the lower; pedicel articulation always well-marked . **XII Demissa** (in part) (p. 117)

20. Corolla white, pentagonal; plant covered with dense glandular pubescence of an unpleasant odour; tubers developed serially, as periodic swellings on stolon ("string of beads") (Mexico) **XIV Polyadenia** (in part) (p. 125)

Plant without the above combination of characters . 21

21. Corolla lobes rounded and acumens large, so giving the corolla a circular appearance with acumens standing out sharply from it 22

Corolla not as above 23

22\. Leaf pinnate ; interjected leaflets present (Mexico, U.S.A.) **XIII Longipedicellata** (p. 121)

Leaf pinnatisect ; interjected leaflets absent ; wedge-shaped wings on rhachis (S. America) **XV Cuneoalata** (in part) (p. 127)

23\. Corolla sub-stellate, the lobes broadly triangular and acumens not clearly delimited from lobes (lobes as broad as long) 24

Corolla pentagonal or rotate, not sub-stellate **XVII Tuberosa** (in part) (p. 132)

24\. Plants low-growing ; terminal leaflet or lobe much larger than laterals ; peduncle not bifurcate ; articulation high **XV Megistacroloba** (p. 128)

Plants without the above combination of characters . 25

25\. Plant with well-marked wings on rhachis . . . 26

Plant with unwinged rhachis **XVII Tuberosa** (in part) (p. 132)

26\. Rhachis wings wedge-shaped, diminishing gradually in a basiscopic direction from one leaflet to the next lower one **XIV Cuneoalata** (in part) (p. 127)

Rhachis wings more or less parallel-sided or irregular **XVI Ingaefolia** (p. 131)

SERIES I *JUGLANDIFOLIA* RYDB.

(Bull. Torr. Bot. Cl., **51**, 146, 173, 1924)

Plants with herbaceous to woody stems, bright yellow flowers and no stolons or tubers. They are included with the true potatoes because of the position of the pedicel articulation at some distance above the base. They bear obvious resemblances both to section *Neolycopersicon* (*S. pennellii*) and to the genus *Lycopersicon* in their morphology, differing from both in the absence of floral bracts and from *Lycopersicon* in the absence of sterile anther tips. Distribution : Mountains of Central America and north-western South America as far south as the coastal ranges of Peru and north Chile.

Key to species

1. Leaf irregularly bi-pinnatisect ; plant herbaceous or bushy, no more than 2·5 m. tall 2
   Leaf pinnate ; plant a perennial woody climber (liane), much more than 2·5 m. tall 3
2. Plant glandular-pubescent throughout ; stem woody, at least near the base . . . . **2. S. lycopersicoides**
   Plant glabrous, fleshy-leaved, herbaceous . **4. S. rickii**
3. Leaf rugose, hispid above ; interjected leaflets few to absent ; berries not more than 4·5 cm. diam. **1. S. juglandifolium**
   Leaf smooth, velvety ; interjected leaflets frequent ; berries up to 6 cm. diam. . . **3. S. ochranthum**

1. S. juglandifolium Dun. (Synopsis, Montpellier, 6, 1816)
S. lehmannianum Bitt. (in Fedde, Repert., **10**, 532-33, 1912)
S. juglandifolium Dun. subsp. *cundinamarcae* Bitt. (in Fedde, Repert., **12**, 58-59, 1913)

A perennial woody climber (liane) ; leaf pinnate, rugose and hispid above ; interjected leaflets few or absent ; fruit up to 4·5 cm. diam. Distribution : Costa Rica, Venezuela, Colombia, Ecuador. Forests, scrub woodland and hedges at 1,000-3,000 m. 2n = 24.

2. S. lycopersicoides Dun. (in DC. Prodr., **13**, I, 38, 1852)

A bush or shrub, to 2·5 m. tall. Leaf bi-pinnatisect, very similar to that of the tomato. Distribution : Peru. Open ground, from 2,800-3,150 m. 2n = 24.

3. S. ochranthum Dun. (Synopsis, Montpellier, 6, 1816)
S. caldasii Dun. (Synopsis, Montepellier, 6, 1816)

Habit as for *S. juglandifolium* ; leaf pinnate, smooth and velvety ; interjected leaflets very numerous. Very large berries to 6 cm. diam., resembling a green tomato, though much harder. (Forms known to plant breeders under the name of *S. caldasii*, or *S. caldasii* v. *glabrescens* do not belong here, but are classed with *S. chacoense* q.v.) Distribution : Colombia, Ecuador, Peru. Forests, scrub woodland and hedges at 1,800-3,500 m. 2n = 24.

4. S. rickii Correll (Wrightia, **2**, 177-78, 1961)

A herb to 50 cm. tall, glabrous, with bi-pinnatisect leaves and stellate flowers; pericarp rapidly becoming dry and papery at maturity. (Material not examined by me.) Distribution: North Chile. Rocky dry ravines at 3,000 m. 2n = 24.

SERIES II *ETUBEROSA* JUZ.

(Bull. Acad. Sci., U.R.S.S., **2**, 301, 1937, *nomen nudum*; *ex* Buk. & Kameraz, Bases of Potato Breeding, 18, 1959)

Herbs with very low almost basal pedicel articulation, but without the " bayonet hairs " typical of subsection *Basarthrum*. The plants bear no stolons or tubers, though they are sometimes rhizomatous. Corolla rotate, purplish or blueish. Distribution: Central Chile as far south as the island of Chiloé; Nahuel Huapi region of S. Argentina; Islands of Juan Fernandez.

Key to species

1. Pedicel articulated completely at the base; calyx, stem and leaf glabrous or glabrescent. (Juan Fernandez Islands) **3. S. fernandezianum**

Pedicel articulated above the base; plant rarely completely glabrous or glabrescent. (Mainland of Chile and Argentina) 2

2. Calyx with acumen completely absent or not more than 0·5-1 mm. long 3

Calyx with well-developed acumen, 1-2 mm. long or more 4

3. Pedicel articulation $\frac{1}{4}$ to $\frac{1}{3}$ above the base; anthers minutely puberulent externally (maritime marshes) **4. S. palustre**

Pedicel articulation lower, 2-4 mm. above the base; anthers not puberulous . . . . . **1. S. brevidens**

4. Plant small, less than 20-30 cm. tall, subglabrous; interjected leaflets none (very occasionally one) **5. S. subandinum**

Plant larger, pubescent, with fairly numerous interjected leaflets (always more than three) . **2. S. etuberosum**

1. S. brevidens Phil. (Anal. Univ. Chile, Santiago, **43**, 521, 1873)

S. pearcei Phil. (Anal. Univ. Chile, Santiago, **91**, 5-6, 1895; non *S. pearcei* Britton ex Rusby in Mem. Torr. Bot. Cl., **4**, 227, 1895)

S. bridgesii A. DC. (Arch. Sci. Phys. & Nat., Ser. 3, **15**, 437, 1886; non *S. bridgesii* Phil. in Linnaea, **33**, 203, 1864-65)

A highly polymorphic species with pubescence varying from dense to almost absent; pedicel articulation 2-4 mm. above the base; calyx teeth very short (0-0·5 mm.); corolla sky-blue, paling to white at edges. Distribution: S. Central Chile, island of Chiloé, Nahuel Huapi region of S. Argentina. Wet forests from sea level to about 1,000 m. 2n = 24.

NOTE.—A collection incorrectly identified by Dunal as *S. caldasii* var. *glabrescens* belongs to *S. brevidens*; nevertheless, the material known to plant breeders under the name of *S. caldasii* v. *glabrescens* should be referred to *S. chacoense* (q.v.).

2. S. etuberosum Lindl. (Bot. Reg., **20**, t. 1712, 1835)

S. bustillosii Phil. (Linnaea, **29**, 24, 1857/8)

S. looseri Juz. (Bull. Acad. Sci. U.R.S.S., **2**, 301-02, 1937)

Distinguished by yellowish-green stems and leaves, with short velvety pubescence and often crisped leaflet margins; pedicel articulation 4-5 mm. above the base; calyx with well marked teeth (1-1·5 mm.); corolla rich purple, very showy. Distribution: N. Central Chile. Dry mountain forests, from 1,250-2,500 m. 2n = 24.

3. S. fernandezianum Phil. (Linnaea, **29**, 23-24, 1857/8)

Plant glabrous or glabrescent; pedicel articulation right at the base. Distribution: Islands of Juan Fernandez. Wet forests, from 100-600 m. 2n = 24.

4. S. palustre Poepp. (Ex Schlechtd. Hort. Halensis, **1**, 5, 1841)

Plant with a very dense white indumentum mostly of glandular hairs; pedicel articulation 1/4 to 1/3 above the base; anthers minutely puberulent externally. Distribution: Chile. Sea marshes near Valparaiso, rare or possibly extinct.

5. S. subandinum Meigen (Bot. Jahrb., **17**, 293, 1893; *non S. subandinum* Phil., Anal. Univ. Chile, Santiago, **91**, 13-14, 1895)
S. kunzei Phil. (Anal. Univ. Chile, Santiago, **91**, 6-7, 1895)

Small plants (20-30 cm. high or less), subglabrous and rarely with interjected leaflets; calyx acumens fairly well developed. Probably closely related to *S. etuberosum*. Distribution: Chile. Mountain woods and rocks near Santiago at 1,700-2,300 m. (NOTE.—Chromosome number (2n = 48) reported in U.S.D.A. Bulletin 533, **20**, 1958 is probably an error, since this species has not yet been studied in the living state so far as I am aware.)

SERIES III *MORELLIFORMIA* HAWKES

(Scottish Plant Breed. Sta. Ann. Report, 54, 1956)

Small tuber-bearing herbs with a strong resemblance to *S. nigrum*, with predominantly epiphytic habit, simple leaves, very small white stellate flowers (less than 1·5 cm. diam.), long slender anthers which are slightly coherent laterally, and small few-seeded berries. Distribution: Mountain forests of Mexico and Guatemala. This series, formerly united with *Bulbocastana* Rydb., has been separated on account of the very characteristic flowers. It differs from *Bulbocastana* also in its serological reactions (Gell, Hawkes & Wright, 1960).

1. S. morelliforme Bitt. et Muench (in Fedde, Repert., **12**, 154-55, 1913)

A small epiphyte growing on trees and also on moss-covered walls and rocks in dense shade, never on the ground. Distinguished by the simple leaves, small stellate flowers, slender anthers and small, few-seeded berries. Distribution: Central to south Mexico; Guatemala. In wet mountain forests from about 2,000 to 3,000 m. 2n = 24.

SERIES IV *BULBOCASTANA* RYDB.

(Bull. Torr. Bot. Cl., **51**, 146, 172, 1924)

CLARA Graham & Dionne (*ex* Correll, Texas Res. Found. Contrib., **4**, 243, 1962)

Small tuber-bearing terrestrial herbs with simple leaves, stellate flowers (1·5-3 cm. diam.), short thick anthers and round berries, larger than those of *Morelliformia*. Distribution: Central and south Mexico; Guatemala.

Key to species

Corolla lobes white to deep cream; leaves ± cuneate at base, not truncate; base of anther 2-lobed **1. S. bulbocastanum**

Corolla lobes purple at tip; leaves broadly ovate to cordate, truncate to cordate at base; base of anther 3-5-lobed **2. S. clarum**

1. S. bulbocastanum Dun. (in Poir. Encycl. Suppl. **3**, 749, 1813)

Leaf with rounded to cuneate base, generally densely pubescent, varying from ovate to linear-lanceolate according to subspecies. Flowers white to deep cream. Both diploid and (apparently) autotriploid forms are known.

Subspecies bulbocastanum. Leaf and stem densely pubescent; leaf ovate in shape, less than 2·5 times as long as broad; corolla white. Central to south Mexico.

Subspecies dolichophyllum (Bitt.) Hawkes, comb. nov.

S. bulbocastanum var. *dolichophyllum* Bitt. (in Fedde, Repert., **11**, 447, 1912)

S. longistylum Corr. (U.S. Dept. Agric. Monogr. No. 11, 87, 1952)

Leaf linear-lanceolate, more than 2·5 times as long as broad, attenuate at base and apex; style varying in length from 6 to 10 mm. Corolla white. Central Mexico, States of Morelos and Guerrero.

Subspecies partitum (Corr.) Hawkes, comb. nov.

S. bulbocastanum var. *partitum* Correll (U.S. Dept. Agric. Monogr. No. 11, 83, 1952)

Leaf ovate to ovate-lanceolate, less than 2·5 times as long as broad; leaf and stem less densely pubescent than in subsp. *bulbocastanum*; pedicel above articulation and calyx completely glabrous; calyx pale yellow-green; corolla deep cream, the lobes very deeply separated from each other. Guatemala and the State of Chiapas in Mexico.

General Distribution: Central to south Mexico; Guatemala. Woods, grassland, rocks and field borders. Often grows under quite dry conditions. Altitude range 1,500-2,300 m. 2n = 24, 36.

2. S. clarum Corr. (Texas Res. Found. Contrib., **1**, 10-12, 1950)

Leaves typically cordate; corolla lobes purple above, white below; base of anther 3-5-lobed. Distribution: Guatemala, depts. Huehuetenango and Quezaltenango. High mountain forests. 2n = 24.

SERIES V *PINNATISECTA* RYDB.

(Bull. Torr. Bot. Cl., **51**, 146, 167, 1924)

CARDIOPHYLLA Buk. (*ex* Correll, U.S. Dept. Agric. Monogr. No. 11, 92, 1952)
TRIFIDA Corr. (Texas Res. Found, Contrib., **1**, 12, 1950)

Herbs with stolons and tubers, imparipinnate to imparipinnatisect leaves and stellate corolla which is white or deep cream coloured, sometimes tinged with purple; berries globular to conical. Further knowledge of the three series cited above has made it impossible to maintain them as distinct entities; even the conical berry which was thought by Correll to be one of the most distinctive features of series Trifida is not such a useful diagnostic character as was at first hoped. At least one form of *S. pinnatisectum* also possesses a conical fruit, and the same mixing of conical and round-fruited species can be seen in other series, such as Demissa and Polyadenia. Distribution: United States (Colorado) southwards to Central Mexico.

Key to species

1. Pseudostipular leaves pinnately lobed, or absent, never clasping the stem 2
   Pseudostipular leaves falcate or semi-lunate, clasping the stem 3

2. Leaves glabrous; leaflets linear-lanceolate, 6-8 paired; corolla lobes only slightly longer than broad **5. S. pinnatisectum**

Leaves with generally a few hairs; leaflets lanceolate, 2-3(-5)-paired; corolla lobes much longer than broad **3. S. jamesii**

3. Leaflets ± petiolulate, generally not decurrent, but if so with decurrent wings running down the petiolule on to the rhachis; corolla lobes fairly narrow 4

Leaflets sessile, slighty decurrent on to the rhachis; corolla lobes broader 7

4. Leaflets petiolulate and decurrent 5

Leaflets distinctly petiolulate, not decurrent . . 6

5. Leaflets 4-5-paired; plant glabrous **6. S. x sambucinum**

Leaflets 2-3(-4)-paired; plant with very short 2-3-celled hairs, visible only under a lens **1. S. brachistotrichum**

6. Calyx acumens 2·5 mm. long; inflorescence a many-flowered diffuse cymose panicle . **8. S. hintonii**

Calyx acumens very short, never more than 1·5 mm. long; inflorescence condensed, of usual type **2. S. cardiophyllum**

7. Leaflets at least 6 times as long as broad, sub-linear **7. S. stenophyllidium**

Leaflets 2-4 times as long as broad, ovate-lanceolate to ovate-oblong 8

8. Leaf 3-4-jugate; plant with dense pubescence and 2-3-celled hairs on lower corolla surface **9. S. nayaritense**

Leaf 1-3-jugate; leaflets sparsely pubescent on lower surface; corolla ± glabrous below **4. S. michoacanum**

1. S. brachistotrichum (Bitt.) Rydb. (Bull. Torr. Bot. Cl., **51**, 170, 1924)

Distinguished from all other species in this series by the characteristic minute 2-3-celled triangular hairs on leaves and stem. Leaflets subsessile to petiolulate, always slightly decurrent on to rhachis, 2-3(-4)-jugate. Corolla slightly mauve-tinted towards acumens, very reflexed. Distribution: N.W. Mexico. Dry piñon and juniper scrub vegetation at 1,750-2,500 m. 2n = 24.

2. S. cardiophyllum Lindl. (J. Hort. Soc., **3**, 70, 1848; non *S. cardiophyllum* Dun. in DC Prodr., **13**, I, 89, 1852)

S. coyoacanum Buk. (*apud* Rybin, Bull. Appl. Bot., **20**, 700, 1929)

Leaflets ovate-cordate to lanceolate, 2-4-jugate, petiolulate, not decurrent (or only occasionally so); calyx acumens 0.5-1.5 mm. long, according to subspecies.

Subspecies cardiophyllum. Leaflets glabrous, shining, dark green above; calyx acumens not more than 0.5 mm. long; corolla deep cream to buff-coloured. Anthers short, 5 mm., not attenuate above, often tinged with violet inside. Both diploid and (apparently) autotriploid forms are known, the latter being distinguished generally by very much wider (broadly ovate-cordate) leaflets. Most of the material mentioned in the plant-breeding literature as *S. lanciforme* should more correctly be considered as the diploid form of subsp. *cardiophyllum*.

Subspecies ehrenbergii Bitt. (in Fedde, Repert., **11**, 442-43, 1912)

S. ehrenbergii (Bitt.) Rydb. (Bull. Torr. Bot. Cl., **51**, 169-70, 1924)

Differs from the type subspecies by the paler green, non-shining, oblong-lanceolate to lanceolate leaflets and the frequent presence of hairs of varying lengths on leaves and stems. Calyx acumens 1-1.5 mm. long; anthers narrow, generally attenuate. Petals often tinged with mauve towards the tips. This subspecies is linked to subspecies *cardiophyllum* in Querétaro State by a series of intermediates. Mostly diploid forms are known, though a triploid (presumably autotriploid) has been recorded in San Luis Potosí State.

Subspecies lanceolatum (Berth.) Bitt. (in Fedde, Repert., **11**, 440-42, 1912)

S. lanceolatum Berth. (Ann. Sci. Agron., ser. 3, **6**, 201-02, 1911; non *S. lanceolatum* Cav. Ic. **3**, 23, t. 245, 1794)

S. lanciforme Rydb. (Bull. Torr. Bot. Cl., **51**, 169, 1924)

This does not differ sufficiently from the diploid forms of subsp. *cardiophyllum* to be ranked as a separate species. Distinguished from subsp. *cardiophyllum* by the narrower leaflets (more than 2.5 times as long as broad), the longer peduncle (more than 3.5 cm. long) and the 0.5-1.0 mm. long calyx acumens. Corolla white or cream-coloured.

Distribution: Subspecies *cardiophyllum*: Central Mexico (States of Mexico, D.F., Morelos, Hidalgo, Puebla). Subspecies *ehrenbergii*: Central to N.W. and W. Mexico (States of Querétaro, San Luis Potosí, Guanajuato, Jalisco, Aguas Calientes, Zacatecas, Michoacán, Hidalgo). Subspecies *lanceolatum*: Central to S. Mexico (States of Hidalgo, Puebla and Oaxaca). All subspecies occur in dry scrub vegetation in waste places, field borders, old lava fields, and especially as weeds of cultivation; the tubers of subsp. *ehrenbergii* are edible. Alt.: 1,600-2,550 m. 2n = 24, 36.

3. S. jamesii Torr. (Ann. Lyc. N. York, **2**, 227, 1828)

Plants without typical semilunate pseudostipular leaflets; if present they are pinnatisect and do not clasp the stem. Leaves slightly decurrent, generally pubescent, occasionally glabrous, with (2)-3-4-(5) pairs of leaflets and generally no interjected leaflets. Corolla lobes narrow. Distribution: N.W. Mexico; S.W. United States; dry scrub vegetation from 1,500-2,300 m. 2n = 24.

4. S. michoacanum (Bitt.) Rydb. (Bull. Torr. Bot. Cl., **51**, 171, 1924)

S. trifidum Corr. (Texas Res. Found. Contrib., **1**, 12-14, 1950)

Leaf 1-3-jugate; stem softly pubescent, provided with hairs and glands; corolla creamy white, with fairly broad lobes. Berries long oval, pointed. In my opinion this is a good species (not a hybrid, as Correll affirms) and is completely synonymous with *S. trifidum*, which Correll places in another series. Distribution: Western Mexico (States of Michoacán and Jalisco), in open pine forests, maize fields, roadsides, &c., at altitudes of 2,100-2,400 m. 2n = 24.

5. S. pinnatisectum Dun. (in DC. Prodr., **13**, I, 40, 1852)

Plant without semilunate pseudostipular leaflets, as in *S. jamesii*. Distinguished from *S. jamesii* by the glabrous leaves, 6-8 leaflet pairs, generally with a few interjected leaflets and large showy corolla with broad triangular lobes. Berry round to conical. Distribution: Central Mexico. Cultivated fields, waste places and field borders, from 1,800-2,100 m. 2n = 24.

6. S. × sambucinum Rydb. (Bull. Torr. Bot. Cl., **51**, 169, 1924)

A natural hybrid between *S. pinnatisectum* and *S. cardiophyllum* susbp. *ehrenbergii*, which shows segregation to the parental types when grown from seed. Leaf fairly dark green, with 4-5-paired leaflets which are narrowly lanceolate and both petiolulate and decurrent (thus intermediate between the two parents). Corolla with lobes broader than those of *S. cardiophyllum*, narrower than those of *S. pinnatisectum* (5-6 × 10 mm.). Distribution: Central Mexico, States of Querétaro and Guanajuato; a weed of fields and field borders, found in the distribution areas of the two parents, at about 1,800-2,000 m. 2n = 24.

7. S. stenophyllidium Bitt. (in Fedde, Repert., **12**, 51, 1913)

Leaflets at least 6 times as long as broad, sub-linear. Little is known of this species, but it may be an extreme southern form of *S. brachistotrichum*, which in some ways it resembles. Distribution: W. Mexico, State of Jalisco, and perhaps elsewhere. In dry grassy places and scrub at about 2,000 m. 2n = 24, according to Graham and Dionne, though I am doubtful whether the material they examined belonged to this species.

8. S. hintonii Corr. (Wrightia, **2**, 139-41, 1961)

A delicate species, with 3-jugate petiolulate leaflets and rather long peduncle branches, giving the inflorescence the appearance of a diffuse cymose panicle; calyx acumens 2.5 mm. long; corolla lobes narrow lanceolate, occasionally broader at the base. Closely related to *S. cardiophyllum*, and perhaps only an extreme variant, since the inflorescence and leaf are rather similar to some biotypes of subsp. *ehrenbergii*. Distribution: Mexico, Mexico State, by stone walls, at 1,700 m. altitude.

9. S. nayaritense (Bitt.) Rydb. (Bull. Torr. Bot. Cl., **51**, 170, 1924)
S. jamesii subsp. *nayaritense* Bitt. (in Fedde, Repert., **12**, 8-9, 1913)

Distinguished from the other species in the series by the 2-3-celled hairs on the lower corolla surface; leaf 3-4-jugate. Possibly related to *S. michoacanum*. Distribution: W. Mexico, State of Nayarit and possibly elsewhere; probably in mountain pine forests; altitude unknown.

(*S. nicaraguense* Rydb. See Appendix, p. 162.)

SERIES VI *COMMERSONIANA* BUK.

(Bull. Acad. Sci. U.R.S.S., 714, 1938, *nomen nudum* ;
ex Buk. & Kameraz, Bases of Potato Breeding, 19, 1959)

GLABRESCENTIA Buk. (ex Buk. & Kameraz, Bases of Potato Breeding, 19, 1959)

TARIJENSA Corr. (Texas Res. Found. Contrib., **4**, 233, 1962)

YUNGASENSIA Corr. (Texas Res. Found. Contrib., **4**, 220-22, 1962)

Tuber-bearing herbs with imparipinnate leaves and stellate corolla with rather broad lobes, generally less than twice as long as broad. Flowers white or mauve-tinted. Distribution : South America : Bolivia, Argentina, Paraguay, Uruguay, Brazil. All species so far discovered are diploid, though some autotriploid forms occur.

Key to species

1. Anthers not well-delimited from filaments, either in colour or form . . . . . . **5. S. calvescens**
   Anthers sharply delimited from filaments, both in colour and form 2
2. Plant covered with a fairly dense indumentum of stalked glands (visible under lens)—easily seen on pedicels and peduncles even in the dried state ; corolla normally white . . . . . . **3. S. tarijense**
   Plant without a dense glandular indumentum . . 3
3. Lateral leaflets not acuminate, normally obtuse, sessile to subsessile and generally slightly decurrent ; peduncle not or only once-forked ; flowers white or mauve ; berries oval to conical . . . **2. S. commersonii**
   Lateral leaflets acute to acuminate, clearly petiolulate and not decurrent ; peduncle generally twice-forked ; flowers white to pale yellow, berries globular 4
4. Corolla small (2 cm. diam.) with narrow lobes more than twice as long as broad, deep cream or even pale yellow in colour . . . . . **4. S. yungasense**
   Corolla larger, always white, the lobes not more than twice as long as broad . . . . . **1. S. chacoense**

1. **S. chacoense Bitt.** (in Fedde, Repert., **11**, 18, 1912)
S. arnezii Cárd. (Bol. Soc. Peruana Bot., **5**, 37-41, 1956)
S. bitteri Hassl. (in Fedde, Repert., **11**, 190, 1912)
S. boergeri Buk. (Rev. Argent. Agron., **4**, 239, 1937)
S. caipipendense Cárd. (Bol. Soc. Peruana Bot., **5**, 35-36, 1956)
S. cuevoanum Cárd. (Bol. Soc. Peruana Bot., **5**, 36-37, 1956)
S. emmeae Juz. et Buk. (Bull. Acad. Sci. U.R.S.S., **2**, 321-22, 1937)
S. garciae Juz. et Buk. (Rev. Argent. Agron., **3**, 227-28, 1936)
S. gibberulosum Juz. et Buk. (Rev. Argent. Agron., **3**, 225-26, 1936)
S. guaraniticum Hassl. (in Fedde, Repert., **9**, 115, 1911 ; non *S. guaraniticum* A. St Hilaire, in Mem. Mus., **12**, 321-22, 1825)
S. horovitzii Buk. (Rev. Argent. Agron., **4**, 238, 1937)
S. jujuyense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 114, 1944)
S. knappei Juz. et Buk. (Bull. Acad. Sci., U.R.S.S., **2**, 322-23, 1937)
S. laplaticum Buk. (Rev. Argent. Agron., **4**, 238-39, 1937)
S. limense Corr. (Wrightia, **2**, 188-89, 1961)
S. parodii Juz. et Buk. (Rev. Agent. Agron., **3**, 226, 1936)
S. saltense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 113-14, 1944 ; non *S. saltense* C. V. Morton, in Contrib. U.S. Nat. Herb., **29**, 63, 1944)
S. schickii Juz. et Buk. (Bull. Acad. Sci. U.R.S.S., **2**, 324-25, 1937)
S. subtilius Bitt. (in Fedde, Repert., **12**, 6-7, 1913)
S. chacoense subsp. *subtilius* Hawkes (Ann. Rep. Scottish Pl. Breed. Sta., 61, 1956)

Differs from *S. commersonii* in the petiolulate acute to acuminate leaflets, the terminal leaflet hardly larger than the laterals, the uniformly white corolla and the globular berries. An extremely polymorphic species spreading through south Bolivia, north and central Argentina, Paraguay, Uruguay and south Brazil, generally as a field weed in lowland pastures.

The great range of variation has induced many authors to divide it into a large number of microspecies which cannot now be maintained since they are all apparently fertile with each other and intergrade considerably.

A collection known to plant breeders erroneously as "*S. caldasii*" or "*S. caldasii* var. *glabrescens*" must be included as *S. chacoense*; *S. caldasii* is a synonym of *S. ochranthum* (q.v.), whilst the type material of *S. caldasii* var. *glabrescens* belongs to *S. brevidens*.

Subspecies chacoense. Lateral leaflets 2-3 times as long as broad; plains forms are almost glabrous, forming a semi-rosette in the early stages of growth, and also possess very short (not more than 0.75 mm.) calyx acumens. Forms of subsp. *chacoense* occurring in the mountain valleys of N.W. Argentina and south Bolivia are more pubescent, with shorter petiolules, longer calyx acumen and more developed stem wings. They rarely form the semi-rosette of basal leaves that is seen in *S. chacoense* in the plains. These forms seem to be due to introgression with the species *S. microdontum* and possibly certain other mountain species. It has been thought advisable not to give them separate subspecies rank for the time being.

Subspecies muelleri (Bitt.) Hawkes & Hjerting, comb. nov.

S. muelleri Bitt. (in Fedde, Repert., **12**, 155-56, 1913)
S. jamesii Torr. var. *grandifrons* Bitt. (in Fedde, Repert., **12**, 151-52, 1913)

Differs from subsp. *chacoense* by the long narrow leaflets, about 3·3-4·3 times as long as broad, the long petiolules, up to 25 mm. on the acroscopic side, the very oblique leaflet bases and rather low pedicel articulation. Plant generally glabrous, very occasionally pubescent.

Distribution: Subsp. *chacoense*: Bolivia, Argentina, Paraguay, Uruguay. Waysides, pastures, arable land, scrub and woodland margins, from sea level to 2,350 m.

Subsp. *muelleri*: Argentina (prov. Misiones), South Brazil (States of Rio Grande, Paraná, Santa Catarina). Grasslands, river banks, waysides, fields, forest margins and clearings, at fairly low altitudes (up to 800 m.?).

With the exception of one autotriploid collection (CPC: 1720 from Rio de la Plata) the whole of *S. chacoense* is diploid. 2n = 24 (36).

2. S. commersonii Dun. (in Poir. Encycl. Suppl., **3**, 746, 1813)

S. acroleucum Bitt. (in Fedde, Repert., **11**, 435-36, 1912)
S. henryi Buk. & Lechn. (Rev. Argent. Agron., **2**, 182-83, 1935)
S. mechonguense Buk. (Rev. Argent. Agron., **7**, 363, 1940)
S. mercedense Buk. (Soviet Plant Industr. Record, No. 4, 3-12, 1940)
S. ohrondii Carr. (Rev. Hort., **55**, 496-500, 1883)
S. sorianum Buk. (Soviet Plant Industr. Record, No. 4, 3-12, 1940)
S. tenue Sendtn. (in Martius, Fl. Brasil., **10**, 13, 1846)

This very well-known species differs from *S. chacoense* in possessing leaflets which are normally obtusely rounded at the apex, sessile or subsessile and generally slightly decurrent ; the terminal leaflet is typically much larger than the laterals and the leaf is often sublyrate in shape. Peduncle not or once-branched ; branches often very short. Corolla white or often tinted purple on the external surface ; berry cordate or conical. Occurs in both diploid and (probably) autotriploid forms, the latter being confined chiefly to the vicinity of Montevideo in Uruguay and Prov. Misiones in Argentina.

Subspecies commersonii. Lateral leaflets decreasing rapidly to base of leaf, often markedly decurrent, normally sessile ; peduncle once-forked, the branches somewhat contracted ; corolla generally purple, the lobes about 1½ times as long as broad or even longer. Most plant breeding and cytological work in the past has utilized this subspecies, often in its triploid forms ; certain forms of *S. chacoense*, erroneoulsy identified as *S. commersonii*, have been reported on in recent studies by various workers. Typical diploid subsp. *commersonii* has sub-lyrate leaves, elongated and enlarged terminal leaflets and very reduced laterals ; the flowers are deep mauve on the outer surface, paler within. The triploid forms are less typical, with wider, less decurrent, often slightly petiolulate leaflets and terminal leaflet not much larger than laterals. They can be distinguished from *S. chacoense* by the *very short* peduncle branches which make the pedicels appear to be arranged in a cymose umbel. The flowers are almost invariably mauve to purple and the berries (when formed) are cordate and pointed.

Subspecies malmeanum (Bitt.) Hawkes & Hjerting, comb. nov.

S. malmeanum Bitt. (in Fedde, Repert., **12**, 447-48, 1913)
S. millanii Buk. & Lechn. (Rev. Argent. Agron., **2**, 180-82, 1935)
S. pseudostipulatum (Hassl.) Buk. (Rev. Argent. Agron., **2**, 180, 1935)
S. commersonii var. *pseudostipulatum* Hassl. (in Fedde, Repert., **9**, 116, 1911)

Differs from subsp. *commersonii* in the lateral leaflets gradually decreasing to base of leaf, narrowly decurrent and slightly petiolulate; peduncles unbranched or the branches not markedly contracted; corolla always white, the lobes about as long as broad. This subspecies is known in diploid and triploid forms, the latter having been found chiefly in Argentina, prov. Misiones. Like subsp. *commersonii*, it possesses conical berries and is resistant to frost.

Distribution: Subsp. *commersonii*: coastal belt of Argentina and Uruguay (estuary of the Rio Plata), and coastal regions of south Brazil (States of Rio Grande and Santa Catarina). Grows in a wide variety of habitats, but very frequently in marshy places, fields, river banks, woods and sandy shores (dune slacks), from sea level up to about 400 m.

Subsp. *malmeanum* has a more inland distribution and is known in N.E. Argentina (chiefly in provs. Corrientes and Misiones), Brazil (Rio Grande), N. Uruguay and south Paraguay. Inhabits similar places to those in which subsp. *commersonii* is found but seems to prefer shady thickets and woodlands; it has about the same altitude range as subsp. *commersonii*. $2n = 24, 36$.

3. S. tarijense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 114-15, 1944)

S. trigalense Cárd. (Bol. Soc. Peruana Bot., **5**, 41-42, 1956)
S. zudaniense Cárd. (Bol. Soc. Peruana Bot., **5**, 31-32, 1956)

Plant with a dense pubescence of simple and glandular hairs, pleasantly aromatic ; calyx acumens well-marked, linear ; berry globular, with white raised spots. Natural hybridization with blue-flowered mountain species has caused a certain amount of introgression into *S. tarijense* from them. An apparently stable natural hybrid of this type is *S.* × *berthaultii* (see p. 140) from Cochabamba, Bolivia, which may possibly have resulted from *S. tarijense* × *S. sparsipilum* crosses.

Distribution : Bolivia and N.W. Argentina. Scrub and cactus vegetation in dry interandine valleys at altitudes of about 2,000 to 2,800 m. 2n = 24.

4. **S. yungasense Hawkes** (Ann. Mag. Nat. Hist., Ser. 12, **7**, 697, 1954)

Plant with small (2 cm. diam.) pale yellow or deep cream corolla with narrow lobes more than twice as long as broad. This species bears a remarkable vegetative similarity to *S. violaceimarmoratum* (Series Conicibaccata). Distribution: North Bolivia, sub-tropical forests (Yungas region) at 1,100-1,900 m. (May perhaps also be found in Peru.) 2n = 24.

5. **S. calvescens Bitt.** (in Fedde, Repert., **11**, 435-36, 1912)

Is probably related to *S. Commersonii*, and especially to subsp. *malmeanum*, from which it may be distinguished by the larger size, upright growth, curved leaves, more acute lateral leaflets, large flowers, and especially by the curious stamens (see also *S. maglia*) in which the anthers and filaments are not clearly delimited from each other, either in form or colour. Distribution : Brazil, State of Minas Gerais, and perhaps elsewhere ; on shady river banks and in cultivated fields, at altitudes of about 1,200 m.

SERIES VII *CIRCAEIFOLIA* HAWKES

(Ann. Mag. Nat. Hist., Ser. 12, **7**, 702, 1954)

Tuber-bearing herbs with small leaves, the terminal leaflet enlarged and laterals reduced in size. Corolla white, stellate, less than 1.5 cm. diam. ; berries narrow-conical. Distribution : N. Bolivia ; hedges and bushy places at high altitudes.

Key to species

Leaf and inflorescence softly hairy ; leaflets not acuminate **1. S. capsicibaccatum**

Leaf and inflorescence glabrescent ; leaflets acuminate **2. S. circaeifolium**

1. S. capsicibaccatum Cárdenas (Rev. Agric., Cochabamba, **2**, 35-36, 1944)

Distinguished from *S. circaeifolium* by the softly hairy leaves, 1-2 pairs of lateral leaflets which are more than half the length of the terminal, rather pubescent inflorescence and grooved stigma. Distribution : Bolivia, depts. Cochabamba, Santa Cruz and La Paz, in cloud forest and among bushes and scrub vegetation at 2,000-4,000 m. altitude. $2n = 24$.

2. S. circaeifolium Bitt. (in Fedde, Repert., **11**, 385-86, 1912)

Leaf glabrescent, simple, or sometimes 1-2-jugate, the laterals much less than half the length of the terminal leaflet ; stigma simple. Distribution : Bolivia, dept. La Paz, Cochabamba, in cloud forest and scrub vegetation at altitudes of 2,500-3,900 m. $2n = 24$.

SERIES VIII *CONICIBACCATA* BITT.

(in Fedde, Repert., **11**, 381, 1912)

OXYCARPA Rydb. (Bull. Torr. Bot. Cl., **51**, 146, 172, 1924)

Tuber-bearing herbs with generally well-dissected leaves and acuminate leaflets, rotate to ± stellate, whitish to generally purple flowers and ovate-conical to long conical berries. Geographical distribution : Mexico, southwards to Bolivia ; all species grow in humid mountain forests and in other regions of high rainfall.

Conicibaccata is the only taxonomic series of wild potatoes to be found both north and south of the Panamá isthmus (with the possible exception of Juglandifolia and Tuberosa). Many of the species are not very well known and are difficult to cultivate. With better knowledge it will probably be necessary to reduce some species to synonymy, whilst others may need to be removed to other series. The polyploid series of species in Conicibaccata, with diploid, tetraploid and hexaploid species, is of great theoretical interest and indicates a possibly rather complex evolutionary history, of which practically nothing is yet known.

Key to species known in the living state

1. Terminal leaflet 1½ times or more wider than laterals . 2
   Terminal leaflet less than 1½ times as wide as laterals . 3
2. Corolla stellate ; pedicel gradually swelling into calyx base ; stem generally marbled **7. S. violaceimarmoratum**
   Corolla ± rotate ; pedicel sharply delimited from calyx base ; stem not marbled **2. S. colombianum** (in part)
3. Berries pointed, narrowly conical or elliptic-conical, 3-4 cm. long when mature and twice as long as broad . . 4
   Berries broadly ovate-conical with rather blunt apex, less than 3 cm. long when mature, never more than twice as long as broad 5
4. Leaf with (6-)7-9 pairs of lateral leaflets and frequent interjected leaflets . . . **1. S. agrimonifolium**
   Leaf with not more than 5 pairs of lateral leaflets and 3 pairs of interjected leaflets . . . **4. S. oxycarpum**
5. Whole plant covered with dense short shining pubescence ; leaf 2-(3-) jugate . . . **6. S. urubambae**
   Pubescence not of this type 6
6. Corolla stellate or nearly so ; leaves acuminate **5. S. santolallae**
   Corolla rotate ; leaves not or barely acuminate . . 7
7. Corolla with flattened or even concave lobes, appearing somewhat 10-pointed . . . . **3. S. moscopanum**
   Corolla rotate-pentagonal ; lobes not flattened or giving a 10-pointed appearance **2. S. colombianum** (in part)

1. S. agrimonifolium Rydb. (Bull. Torr. Bot. Cl., **51**, 154, 1924)

Berries narrow-conical, grooved, 3-4·5 cm. long. Leaf with (6-)7-9 pairs of leaflets and numerous interjected leaflets.

Distribution : S. Mexico to Guatemala. Cloud forests at about 2,000-3,300 m. 2n = 48.

2. S. colombianum Dun. (in DC. Prodr., **13**, I, 33, 1852)

S. dolichocarpum Bitt. (in Fedde, Repert., **12**, 4-5, 1913)
S. filamentum Corr. (Wrightia, **2**, 174-75, 1961)
S. otites Dun. (in DC. Prodr., **13**, I, 39, 1852)

Corolla rotate-pentagonal ; berries broadly ovate-conical with generally blunt apex, less than 3 cm. long ; leaves barely acuminate. A very polymorphic species occurring in Venezuela, Colombia and Ecuador. Cloud forests at 2,200-3,500 m. 2n = 48.

3. **S. moscopanum Hawkes** (Ann. Mag. Nat. Hist., Ser. 12, **7**, 689-90, 1954)

Corolla with flattened or even slightly concave lobes, appearing somewhat 10-pointed. Berries and leaves similar to *S. colombianum* from which this species was probably in part derived. Distribution : S. Colombia. High altitude forests and clearings at 2,900-3,400 m. 2n = 72.

4. S. oxycarpum Schiede (in Schlechtd., Hort. Halensis, **1**, 5, 1841)

S. longiconicum Bitt. (in Fedde, Repert., **10**, 534, 1912)
S. manoteranthum Bitt. (in Fedde, Repert., **11**, 383-84, 1912)

Berries narrow-conical, 3-4 cm. long, sharp-pointed ; leaflets acuminate ; interjected leaflets generally absent ; corolla rotate. Distribution : Mexico to Panamá (not recorded for Guatemala). Cloud forests at about 1,500-3,200 m. 2n = 48.

5. S. santolallae Vargas (Rev. Argent. Agron., **10**, 397, 1943)

S. claviforme Corr. (Wrightia, **2**, 174, 1961)

Distinguished by the more or less stellate whitish corolla, long-acuminate leaflets and ovate-conical berries which are 2-2.5 cm. long. Distribution : South and Central Peru.

Growing in cloud forests, thickets and clearings at 2,500-3,600 m. 2n = 24.

6. S. urubambae Juz. (Bull. Acad. Sci. U.R.S.S., **2**, 312-13, 1937)

Leaf 2-jugate; leaflets oblong-ovate; pubescence dense, short and shining. Distribution: S. Peru, in cloud forests and clearings at 2,000-2,200 m.

7. S. violaceimarmoratum Bitt. (in Fedde, Repert., **11**, 389-90, 1912)

Terminal leaflet much wider, though barely longer than lateral leaflets; leaflets 3-4-jugate; stem often violet-marbled; pedicel swelling into calyx base; corolla stellate. Berries to 2·5 cm. long. Distribution: N. Bolivia, in cloud forests and clearings, pathsides, etc., at 1,800-3,600 m. 2n = 24.

8. S. ayacuchoense Ochoa (Agronomía, Lima, **26**, 312-13, 1959)

Lateral leaflets 3-5-jugate, with very long petiolules (10-20 mm.) and pedicels articulated only one-third above the base; corolla rotate; berries long conical, 2-2.5 cm. long. Distribution: Central Peru (dept. Ayacucho), in cloud forests at 3,000 m. (Material not seen by me.)

9. S. buesii Vargas (Rev. Argent. Agron., **10**, 396-97, 1943)

Leaf with 3(-5) pairs of lateral and 2-3 pairs of interjected leaflets. Calyx conspicuously hirsute. Very similar to *S. santolallae*, of which it may be no more than a slight variant. Distribution: S. Peru, in cloud forests at 2,400-3,600 m.

10. S. jaenense Ochoa (Agronomía, Lima, **27**, 371-72, 1960)

A delicate slender plant with 2-3-jugate acuminate leaflets, white rotate corolla and acute fruits to 10 mm. long. Distribution: Endemic to N. Peru (Cajamarca) at 2,700 m.; habitat unknown. (Material not seen by me.)

11. S. laxissimum Bitt. (Beibl. Bot. Jahrb. No. 119, **54**, 7-8, 1916)

S. rockefelleri Vargas (Papas Sudperuanas, Cuzco, **2**, 54-55, 1956)

Leaf very large, 4-6-jugate; corolla blue, 3-3.5 cm. diam.; filaments pubescent; berries long conical, 2.5-3 cm. long. Distribution: South to Central Peru, growing at the edges of cloud forests, from 1,900-3,000 m.

12. S. multiflorum Vargas (Papas Sudperuanas, Cuzco, **2**, 55-56, 1956)

Leaf 2-3-jugate, covered with coarse shining hairs; inflorescence many-flowered; pedicels articulated near base; corolla pentagonal-rotate; calyx acumens linear to spathulate; berry conical. Distribution: South Peru, growing amongst scrub and bushes, at about 2,100-2,700 m.

13. S. neovargasii Ochoa (Sol. tuber. silv. Peru, Lima, 53-57, 1962)

Leaflets 2-3-jugate; corolla purple, rotate; stamen filaments sparsely pubescent; berry ellipsoid or conical ellipsoid, to 2 cm. long. Distribution: Central Peru, at 2,800 m. amongst shrubby mountain forests. (Material not seen by me.)

14. S. paucijugum Bitt. (in Fedde, Repert., **11**, 431-32, 1912)
S. dolichocremastrum Bitt. (in Fedde, Repert., **12**, 3-4, 1913)
S. flahaultii Bitt. (in Fedde, Repert, **12**, 57-58, 1913)

Terminal leaflet much longer and broader than the 2-3-jugate laterals which decrease rapidly towards base of leaf; corolla rotate, purple; berries blunt ovoid. Distribution: Colombia, Ecuador, N. Peru; mountain forests and pastures at altitudes of about 3,500-3,700 m. and perhaps also lower.

15. S. pillahuatense Vargas (Papas Sudperuanas, Cuzco, **2**, 53-54, 1956)

Leaflets 2-jugate; peduncles and pedicels with spreading dense white hairs; fruit ovoido-conical, 1.5 cm. long. Perhaps related to *S. multiflorum*, since the pedicel articulation is rather low and the pubescence is of the same type. Distribution: South Peru, in forest and scrub at about 2,800 m.

16. S. villuspetalum Vargas (Papas Sudperuanas, Cuzco, **2**, 54, 1956)

Leaf 0-2-jugate, covered with very shining dense silky yellowish hairs. Corolla with long narrow acumens. Berries narrowly conical. A curious species, similar vegetatively to the non-tuberiferous species *S. caripense*, except for the high pedicel articulation. Tubers unknown, but may be formed. Distribution: South Peru, on old cultivation terraces at 2,500 m. and elsewhere.

17. S. woodsonii Corr. (Wrightia, **2**, 137-39, 1961)

Leaflets 2-3-jugate, elliptic to broadly oval and rather blunt; anthers with a median lobe at the base, as well as the two lateral ones. Distribution: Costa Rica, Panamá, Venezuela, 3,150-4,000 m. on high páramos (mountain meadows).

(*S. papa* Val. See p. 163.)

SERIES IX *PIURANA* HAWKES

(Ann. Mag. Nat. Hist., Ser. 12, **7**, 693, 1954)

Tuber-bearing herbs with shining glabrous or glabrescent leaves which become leathery and with revolute margin when dry; corolla large, rotate, showy, blue-purple, white and purple or completely white; berries ovate, with flattened apex. Geographical distribution: Colombia, Ecuador, N. and C. Peru, in a wide range of habitats.

The confines of this series are not clearly agreed upon by different *Solanum* taxonomists, and no doubt with better knowledge it will be necessary to reduce some species to synonymy or remove others to nearly related series. Piurana seems to intergrade into Conicibaccata in the north and into Tuberosa in the south, whilst some of the species included here were placed by Correll in series Ingaefolia. In the present edition I have included a number of white-flowered species with glabrous leaves, since apart from flower colour they seem to belong here fairly well. Some of the species listed here as unknown in the living state may in fact have been grown by Ochoa in Peru, but so far as the writer is aware they have not been mentioned in the literature, except for the formal taxonomic descriptions. Diploid and tetraploid species have been reported.

Key to species

1. Flowers blue to blue-purple 2
 Flowers white or white and lilac, etc. 9
2. Interjected leaflets not present 3
 Interjected leaflets developed, at least in the upper leaves 5
3. Leaf rhachis with well-developed wing, about 1-2 mm. wide . . . . **4. S. jalcae**
 Rhachis unwinged 4
4. Lateral leaflets 1(-2)-jugate (Peru) **7. S. acroglossum**
 Lateral leaflets 2-3-jugate (Ecuador) . **16. S. solisii**
5. Lateral leaflets 4-6-jugate, with frequent interjected leaflets 6
 Lateral leaflets 2-3(-4)-jugate, with few interjected leaflets 7
6. Lateral leaflets elliptic ; calyx dark purple **13. S. moniliforme**
 Lateral leaflets lanceolate ; calyx green **6. S. tuquerrense**
7. Corolla not more than 2.5-3 cm. diam. ; leaflets lanceolate . . . . **5. S. piurae**
 Corolla 3-4.5 cm. diam. ; leaflets elliptic 8
8. Leaflets broadly ovate ; filaments glabrous **14. S. pascoense**
 Leaflets narrow-ovate to ovate-elliptic ; filaments pubescent externally . . **2. S. chomatophilum**

9\. Flowers white and lilac, white and pale blue, etc. . 10
Flowers completely white 12

10\. Leaf with about 1 pair of lateral leaflets or completely simple . . . . . . **15. S. paucissectum**
Leaf with about 4-6 pairs of lateral leaflets . . 11

11\. Calyx acumens linear: calyx trilabiate; corolla white, mottled with lavender . **10. S. cyanophyllum**
Calyx acumens very short; calyx regular; corolla white, with lavender streak on centre of each petal **8. S. albornozii**

12\. Terminal leaflet extremely large, compared with the minute laterals . . . . **3. S. hypacrarthrum**
Terminal and lateral leaflets more or less the same size 13

13\. No interjected leaflets present 14
Interjected leaflets present 15

14\. Lateral leaflets sessile, not decurrent **9. S. cantense**
Lateral leaflets petiolulate *and* decurrent **1. S. chancayense**

15\. Leaflets sessile, decurrent . **17. S. yamobambense**
Leaflets petiolulate 16

16\. Leaflets oblong-elliptic; calyx with some coarse hairs **11. S. huancabambense**
Leaflets lanceolate; calyx glabrous or minutely puberulent on margins only . . . . **12. S. immite**

1. S. chancayense Ochoa (Agronomía, Lima, **26**, 316-18, 1959)

Small glabrous plants with 2-3-jugate lateral leaflets and no interjected leaflets; flowers white. Distribution: Peru; coastal hills (lomas) of Lima and La Libertad, from 150-550 m. 2n = 24.

2. S. chomatophilum Bitt. (Abhandl. Naturwiss. Ver., Bremen, **25**, 246-48, 1924)

Leaf 3-4-jugate with 0-4 pairs of small interjected leaflets; leaflets elliptic or broad lanceolate-elliptic, corolla blue, 4 cm. diam. with short lobes; filaments pubescent externally. Distribution: N. Peru in woods and grassy places, from 2,000-4,000 m. 2n = 24.

3. S. hypacrarthrum Bitt. (in Fedde, Repert., **11**, 367-68, 1912)

Leaf simple or with a few pairs of minute laterals and interjected leaflets; terminal leaflet ± cuspidate at apex; corolla white. Distribution: C. Peru, dept. Lima, in grassland and amongst bushes at 1,800-3,400 m. 2n = 24. (Ross).

4. S. jalcae Ochoa (Agronomía, Lima, **19**, 167-69, 1954)

Leaf 2-3-jugate with winged rhachis and larger terminal leaflet; leaf pigmented purple below; calyx dark purple; corolla blue, with short lobes and very small acumens. Distribution: North Peru, growing on páramos and high alpine pastures from 3,100-3,400 m. Frost resistant, according to Ochoa.

5. S. piurae Bitt. (Beibl. Bot. Jahrb., No. 119, **54**, 5-6, 1916)

Leaf 2-3(-4)-jugate; 1-3 pairs of interjected leaflets; leaflets lanceolate; pedicels 3-5·5 cm. long; corolla blue, to 2·5-3 cm. diam.; filaments glabrous. Distribution: N. Peru, rocky slopes amongst shrubs and grasses at 2,500-3,300 m. 2n = 24.

6. S. tuquerrense Hawkes (Ann. Mag. Nat. Hist., Ser. 12, **7**, 693-97, 1954)

Leaf 4-6(-10)-jugate, glabrous or with long spreading hairs; corolla blue, 2-3·5 cm. diam.; filaments glabrous. Unique amongst tetraploids in being self-incompatible. Distribution: Colombia, Ecuador, on páramos and amongst shrubs at 3,000-3,300 m. 2n = 48.

7. S. acroglossum Juz. (Bull. Acad. Sci. U.R.S.S., **2**, 313-14, 1937)

Lateral leaflets 1-(-2) paired; corolla blue; filaments glabrous. Probably closely related to *S. piurae* and *S. paucissectum*. Distribution: Central Peru; habitat unknown; alt. about 3,000 m.

8. S. albornozii Corr. (Wrightia, **2**, 178-79, 1961)

Leaf with 4-6 pairs of laterals and up to about 12 pairs of interjected leaflets, all narrow-lanceolate; calyx acumens short; corolla white, with lilac streak in centre of each petal. A very distinct species, perhaps forming a link between series Piurana and Conicibaccata. Distribution: South Ecuador, on edges of mountain forests at 2,300 m.

9. S. cantense Ochoa (Agronomía, Lima, **26**, 217-18, 1959)

Lateral leaflets 2-3-jugate, not decurrent, with no interjected leaflets; corolla white, with hooded acumens. Possibly related to *S. chancayense*. Distribution: Central Peru, near Canta, at 2,800 m. Habitat unknown.

10. S. cyanophyllum Corr. (Wrightia, **2**, 180-81, 1961)

Leaf dark blue on lower surface; lateral leaflets 4-5-paired; calyx trilabiate, with linear acumens; corolla white, mottled lavender. (Material not seen by me.) Distribution: Ecuador, in forests at 2,300 m.

11. S. huancabambense Ochoa (Agronomía, Lima, **26**, 109-10, 1959)

Leaflets oblong-elliptic, obtuse, petiolulate; calyx with coarse hairs; corolla white, sub-stellate, the lobes about 9 mm. long × 14 mm. wide. Ochoa thought that this species might belong to series Commersoniana, but although there are some resemblances, the rounded corolla lobes, which are broader than long and are well-delimited from the acumens, indicate that *S. huancabambense* does not belong to that series. It is also very isolated geographically from Commersoniana. Distribution: North Peru, dept. Piura, at 1,800-3,000 m. Habitat unknown.

12. S. immite Dun. (in DC. Prodr., **13**, I, 32, 1852)

S. mathewsii Bitt. (in Fedde, Repert., **12**, 53-54, 1913)

Leaflets lanceolate, petiolulate; calyx glabrescent; corolla large, white, rotate, very showy. Distribution: Central to northern Peru, on stony hillsides, from the coastal Lomas (ca. 150 m.) to 2,500 m.

13. S. moniliforme Corr. (Wrightia, **2**, 182-83, 1961)

Leaflets 3-4-paired with some interjecteds, sessile, elliptic and somewhat decurrent; calyx glabrous, dark purple; corolla lavender with a dark central petal streak. Superficially similar to *S. multiinterruptum*, but distinguished by the complete absence of pubescence. Distribution: N. Peru, moist mountain slopes at 3,900 m.

14. S. pascoense Ochoa (Agronomía, Lima, **26**, 112-13, 1959)

Leaflets 2-3-jugate, with a few interjecteds; corolla blue, showy, 3-4·5 cm. diam. Ochoa and Correll consider that it is closely related to *S. multiinterruptum*. Distribution: Central Peru (habitat unknown) at 3,500-3,600 m. (Material not seen by me.)

15. S. paucissectum Ochoa (Agronomía, Lima, **27**, 365-66, 1960)

Terminal leaflet much larger than the 0-2-paired laterals; corolla lilac or lilac and blue. Said by Correll to be synonymous with *S. acroglossum*, but seems distinct, from an examination of Ochoa's plate and description. (Material not seen by me.) Distribution: North Peru, dept. Piura, in open places and amongst trees, at 3,180 m.

16. S. solisii Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 125-26, 1944)

Leaf 1-2-jugate with no interjected leaflets; leaflets elliptic; pedicels to 2·5 cm. long; corolla blue, to 3·5 cm. diam.; filaments glabrous. Distribution: S. Ecuador, in bushy and grassy places on páramos, at 3,500-4,000 m.

17. S. yamobambense Ochoa (Agronomía, Lima, **27**, 367-68, 1960)

Lateral leaflets 3-4-paired, sessile, decurrent, the lower much smaller than the upper ones on each leaf; corolla white with pigmented acumen tips. This species has a strong resemblance to *S. acroglossum*, with which it may perhaps be synonymous. Distribution: N. Peru, amongst dense undergrowth, at 3,160 m.

SERIES X *ACAULIA* JUZ.

(Bull. Acad. Sci. U.R.S.S., **2**, 316, 1937, *nomen nudum* ; ex Buk. & Kameraz, Bases of Potato Breeding, 21, 1959)

Low rosette-forming herbs (occasionally forming long stems), bearing stolons and tubers ; leaves with typically obtuse leaflets auricled at the base on the acroscopic side ; peduncle very short or absent ; pedicel articulation absent or shown only by a ring of pigment, very rarely well-marked ; corolla small, rotate, with very short lobes. Distribution : Peru, Bolivia and N.W. Argentina at very high altitudes in alpine meadows, field borders, etc.

1. S. acaule Bitt. (in Fedde, Repert., **11**, 391-93, 1912)

S. depexum Juz. (Bull. Acad. Sci. U.R.S.S., **2**, 317-18, 1937)

S. uyunense Cárd. (Bol. Soc. Peruana Bot., **5**, 33-35, 1956)

Characters and distribution as for series. The fairly wide infraspecific variation has caused certain authors to split *S. acaule* into several microspecies. The fertility and range of variability between all forms so far studied makes it advisable, however, to reunite them into the one original species, divided into geographical subspecies, as follows :—

Subspecies acaule

Lateral leaflets not very much shorter than terminal leaflets, not or only slightly decurrent ; pedicel articulation generally invisible or marked by a difference of colour ; pubescence of fairly short crisped hairs. 2n = 48.

Subspecies aemulans (Bitt. & Wittm.) Hawkes & Hjerting, comb. nov.

S. aemulans Bitt. & Wittm. (in Engler's Bot. Jahrb., **50**, 553-55, 1914)

S. depexum var. *chorruense* Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 23, 1944)

Differs from subsp. *acaule* in the short leaf with much enlarged terminal and 0-4 pairs of decurrent laterals ; pedicel articulation well-marked but not abscissing when mature. Pubescence as for subsp. *acaule*. 2n = 48 (24, according to Brücher).

Subspecies punae (Juz.) Hawkes & Hjerting, comb. nov.

S. punae Juz. (Bull. Acad. Sci. U.R.S.S., **2**, 316-17, 1937)

Leaf like that of subsp. *acaule*, but stem very short ; pubescence of long weak spreading hairs ; articulation of pedicel never visible except by a change of colour, observable on living plant only. 2n = 48.

Subspecies albicans (Ochoa) Hawkes, comb. nov.

S. acaule Bitt. var. *albicans* Ochoa (Agronomía, Lima, **27**, 363-64, 1960)

Plant apparently similar to subsp. *acaule*, but provided with a dense covering of long white spreading hairs ; corolla very pale, almost white. This subspecies is possibly an amphiploid hybrid of *S. acaule* with a diploid wild species from some other series. (Material not seen by me.) 2n = 72.

Distribution : Subsp. *acaule* : S. Peru, Bolivia, N.W. Argentina, from 2,600-4,650 m., in alpine meadows, by paths, walls, drainage ditches, cultivated fields, etc.

Subsp. *aemulans* : N.W. Argentina, from 2,950-4,000 m in similar habitats to subsp. *acaule*.

Subsp. *punae* : C. Peru, perhaps to N. Peru ?, at similar altitudes and habitats to subsp. *acaule*.

Subsp. *albicans* : N. Peru ; on the páramos or alpine meadows, at 3,450 m. and perhaps elsewhere.

SERIES XI *DEMISSA* BUK.

(Bull. Acad. Sci. U.R.S.S., 715, 1938, *nomen nudum* ;
ex Buk. & Kameraz, Bases of Potato Breeding, 27, 1959)

A rather heterogeneous group of tuber-bearing species characterized chiefly by the high pedicel articulation and rotate corolla with very short lobes, similar to those of *Acaulia*. It is probably linked with *Tuberosa* through the diploid species *S. verrucosum* and has been considered by some authors not to be distinct from *Tuberosa*. Distribution: Mexico and Guatemala. Only diploids, pentaploids and hexaploids are known.

Key to species

1. Corolla with very well-marked interpetalar membranes, so that lobes appear almost flat 2
Corolla with lobes rounded or sloping away steeply from the acumen 7
2. Berries elongate-conical or pointed-oval ; frequent . 3
Berries round ; frequent or rarely produced . . . 4
3. Leaf 2-4-(rarely to 6-)jugate ; very few (0-3) pairs of interjected leaflets present . . **5. S. iopetalum**
Leaf well-dissected, with 5 pairs of laterals and up to 8 or more pairs of interjected leaflets . **3. S. guerreroense**
4. Lateral leaflets sessile or sub-sessile ; terminal leaflets larger than laterals ; peduncle short . . . 5
Lateral leaflets petiolulate ; terminal leaflets about the same size as laterals ; peduncle longer . . . 6
5. Leaf pubescence coarse, white, easily visible to the naked eye ; stem always well-developed ; berries rare or none **6. S. × semidemissum**
Pubescence not easily visible ; stem poorly developed or if long, showing several inflorescences from the base upwards ; berries frequent . . **1. S. demissum**
6. Leaf highly dissected, 4-6-jugate, with up to 9 pairs of interjected leaflets . . . **2. S × edinense**
Leaf poorly dissected, (1-)2-4-jugate, with 1-2 pairs of interjected leaflets . . . **6. S. × semidemissum**
7. Corolla lobes rounded, with involute sides . . . 8
Corolla lobes flat and sloping 9
8. Sepals short ; berry verrucose . . **7. S. verrucosum**
Sepals long acuminate ; berry smooth **8. S. leptosepalum**
9. Corolla white, sometimes with purple splashes ; acumens rather large ; plant tall . . **4. S. hougasii**
Corolla purple ; acumens smaller ; plant dwarf **1. S. demissum** (aberrant form)

1. S. demissum Lindl. (J. Hort. Soc., **3**, 68-70, 1848)

S. alpicum Standl. et Steyerm. (Publ. Field Mus. Nat. Hist., **7**, 232-33, 1947)

S. utile Klotzsch (Allgem. Gart.-Ztg., **17**, 314-16, 1849)

Grows in rosettes or semi-rosettes but sometimes produces a long stem. Leaflets sessile to sub-sessile with rounded apex. Corolla purple, generally with very short lobes. Distribution : Mexico, from Durango State southwards into Guatemala ; pine and fir forests from 2,650-3,800 m. 2n = 72.

2. S. × edinense Berth. (Ann. Sci. Agron., Paris, **2**, 195, 1911)

Includes all forms that have arisen as hybrids between *S. tuberosum* and *S. demissum*. Lateral leaflets petiolulate, 4-6-paired, with up to 9 pairs of interjecteds ; corolla large, with short lobes, much larger than that of *S. demissum*.

Subspecies edinense. Formed as a natural hybrid in the Edinburgh Botanic Gardens and elsewhere, between *S. demissum* and *S. tuberosum* subsp. *tuberosum*.

Subspecies salamanii (Hawkes) Hawkes, comb. nov.

S. salamanii Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 116, 1944)

Formed as a natural hybrid in Mexico, States of Mexico, Vera Cruz, Tlaxcala, etc., from *S. demissum* and *S. tuberosum*, subsp. *andigena* ; leaf much more dissected than in the typical subspecies. Weeds of cultivated fields and waste places, at 2,600-3,500 m. Both subspecies possess 2n = 60 chromosomes.

3. S. guerreroense Corr. (U.S. Dept. Agric. Monogr., No. 11, 65-67, 1952)

Distinguished from *S. demissum* by the conical fruits and from *S. iopetalum* by the well dissected leaves with 5 pairs of primary laterals and 8 or more pairs of interjected leaflets. Stem short ; leaves in a rosette. Distribution : S.W. Mexico, in pine-oak forests at 2,800-3,000 m. 2n = 72.

4. S. hougasii Corr. (Madroño, **14**, 236, 1958)

S. spectabile (Corr.) Hawkes (Ann. Mag. Nat. Hist., Ser. 12, **7**, 701-02, 1954; non *S. spectabile* Steudel, Nomencl. Bot., ed. 2, pt. 2, 606, 1841)

S. verrucosum var. *spectabile* Corr. (U.S. Dept. Agric. Monogr., No. 11, 228, 1952)

Differs from *S. demissum* and *S. guerreroense* in its tall upright habit, white flowers (often tinged purple between petals) longer corolla lobes, and petiolulate leaflets. From *S. iopetalum* and *S. guerreroense* it differs in the corolla form and colour, and in the round berries. Bears some similarities to *S. stoloniferum* in series Longipedicellata. Distribution: West central Mexico; high pine forests or even above the tree line in alpine meadows, from 2,400-4,000 m. 2n = 72.

5. S. iopetalum (Bitt.) Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 30, 1944)

S. verrucosum Schlechtd. var. *iopetalum* Bitt. (in Fedde, Repert., **11**, 455-57, 1912)

S. brachycarpum Corr. (U.S. Dept. Agric. Monogr., No. 11, 59-61, 1952)

S. confusum Corr. (U.S. Dept. Agric. Monogr., No. 11, 63, 1952; non *S. confusum* Morton, Contr. U.S. Nat. Herb., **29**, 70, 1944)

S. demissum Lindl. var. *longibaccatum* Buk. (Bull. Appl. Bot. Genet. Plant Breed, Suppl. 47, 219-20, 1930)

S. nelsonii Corr. (Madroño, **14**, 236, 1958; non *S. nelsonii* Dun., in DC. Prodr., **13**, I, 123, 1852)

S. oxycarpum Schiede var. *brachycarpum* Corr. (Contr. Texas Res. Found., **1**, 8-10, 1950)

S. reconditum Corr. (Wrightia, **2**, 175, 1961)

This very widespread and rather variable species may be clearly distinguished from other species in this series by the upright stems, rather poorly dissected leaves with petiolulate leaflets (generally 2-4, occasionally to 6 pairs of laterals), and few (0-3) pairs of interjecteds; the corolla is large, with short lobes, blue-purple in colour; the berries are conical. Distribution: West, central and south Mexico, in high altitude pine and fir forests at 1,700-3,350 m. 2n = 72.

6. S. × semidemissum Juz. (Bull. Acad. Sci. U.R.S.S., **2**, 314-15, 1937)

Differs from *S. demissum* in the upright habit and petiolulate leaflets, and from *S. × edinense* in the large terminals and poor leaf dissection (2-4-leaflet pairs). Is of undoubted hybrid origin, produced either from a *S. demissum × S. verrucosum* cross (with the participation of an unreduced *S. verrucosum* gamete) or possibly by a *S. demissum × S. stoloniferum* cross. Rarely forms berries. Distribution : C. Mexico ; field weed or along hedges and waysides, sometimes in pine forests, from 2,700-3,500 m. 2n = 60.

7. S. verrucosum Schlechtd. (Hort. Halensis, **1**, 3, 1841)
S. squamulosum Mart. et Gal. (Bull. Acad. Brux., **12**, 1, 140, 1845)

Distinguished by the upright habit, petiolulate leaflets, terminal larger than laterals, well-defined rounded corolla lobes whose margins roll inwards, and white-verrucose berry. Is very probably an ancestral form all *Demissa* species, contributing the one genome that they seem to possess in common. Constitutes a link with series *Tuberosa* and is indeed difficult to separate from it. Distribution : North-east, central and southern Mexico in pine and fir forests at 2,400-3,200 m. 2n = 24.

8. S. leptosepalum Corr. (U.S. Dept. Agric. Monogr., No. 11, 158, 1952)

Apart from the slightly longer calyx acumens and apparently non-verrucose berry this species would seem to be identical with *S. verrucosum* of which it may possibly represent a geographical subspecies. (No authenticated material seen by me.) Distribution : North-east Mexico and possibly Texas, U.S.A., in oak-pine forests at 2,000 m.

SERIES XII *LONGIPEDICELLATA* BUK.

(Bull. Acad. Sci. U.R.S.S., 715, 1938, *nomen nudum* ;
ex Buk. & Kameraz, Bases of Potato Breeding, 27, 1959)

BOREALIA Corr. (Texas Res. Found. Contrib., **4**, 388-90, 1962)

Herbs with long creeping stolons ; leaves with coarse white hairs, or glabrous. The arched corolla lobes and large acumens give the corolla a circular appearance with acumens standing out sharply from it. Corolla occasionally, however, sub-stellate. Distribution : Central Mexico to S.W. United States on dry plateaux and mountain slopes, medium altitudes. Most species are tetraploid.

Key to species

1. Pedicel very densely clothed with white spreading hairs, even above the articulation . **4. S. polytrichon**
   Pedicel sparsely hairy to glabrous, especially above the articulation ; if densely pubescent below articulation then hairs adpressed 2
2. Corolla lobes ± broadly triangular and gradually passing into the acumens 3
   Corolla almost circular in outline, except for the sharply delimited acumens 5
3. Corolla small, never more than 1·5 cm. diam., white with darker acumens ; plants generally not more than 10 cm. tall . . . . **3. S. papita**
   Corolla larger, 2-3 cm. diam., dark purple ; plants generally larger than 10 cm. 4
4. Stem, leaves, peduncle, pedicels and calyx completely glabrous or with one or two small hairs only ; leaflets generally petiolulate . . . . **2. S. hjertingii**
   Stem, leaves, peduncle, pedicels and calyx clothed with frequent coarse hairs ; leaflets normally sessile to sub-sessile . . . . . . **1. S. fendleri**
5. Corolla white to medium purple ; terminal leaflet not differing markedly in size from laterals **5. S. stoloniferum**
   Corolla dark purple ; terminal leaflet broadly obovate to rhomboid, much larger than laterals 6
6. Anthers 5 mm. long ; plant robust (C. Mexico) **6. S. × vallis-mexici**
   Anthers 3 mm. long ; plant small (Arizona) **1. S. fendleri, subsp. arizonicum**

1. S. fendleri A. Gray (Amer. J. Arts & Sci., Ser. 2, **22**, 284-85, 1856)

S. nannodes Corr. (U.S. Dept. Agr. Monogr., No. 11, 161-62, 1952)

Plant with rather dense coarse hairs on leaf, stem, peduncles, pedicels and calyx ; lateral leaflets sessile to sub-sessile, often decurrent ; all leaflets obtuse ; corolla deep purple. Correll's *S. nannodes* seems to be no more than a dry habitat variant of *S. fendleri* ssp. *fendleri*.

Subspecies fendleri. Corolla acumens large, curving gradually into the lobes ; corolla semi-stellate in outline.

Subspecies arizonicum [1] Hawkes, subsp. nov. Differs from subspecies *fendleri* by the rotate corolla with rather small acumens and short lobes, and the small, 3 mm. long anthers.

Distribution : N.W. Mexico and S.W. United States. Subsp. *arizonicum* is apparently endemic to the Chiricahua mountains in S.E. Arizona. *S. fendleri* grows chiefly under the shade of *Pinus ponderosa* and other trees in damp leaf mould at altitudes of 1,700-2,850 m. 2n = 48.

2. S. hjertingii [2] Hawkes sp. nov.

Differs from *S. fendleri* in the glabrous or glabrescent stems, leaves, peduncles, pedicels and calyx, in the generally petiolulate narrow leaflets and the glabrous corolla. Vegetatively extremely similar to *S. cardiophyllum* subsp. *ehrenbergii*, but similar in its floral morphology to *S. fendleri*. Possibly *S. fendleri* var. *physaloides* Corr. should be included under *S. hjertingii*, though the calyx does not become accrescent in the latter species as with var. *physaloides*. Distribution : N.E. Mexico, States of Coahuila and Nuevo León, in dry piñon scrub (*Pinus cembroides*, *Juniperus monosperma*, etc.), at 1,750-2,500 m. in rather similar habitats to *S. jamesii*.

3. S. papita Rydb. (Bull. Torr. Bot. Cl., **51**, 148-49, 1924)

Similar vegetatively to *S. fendleri*, but smaller in its growth (generally not more than 10 cm. tall) and with small corolla (up to 15 mm. diam.) which is whitish with slightly darker acumens. Anthers only 4 mm. long. This species is closely related to *S. fendleri* and may be only a southern subspecies of it ; yet it occurs in different habitats, and intergrading forms are not yet known, though this may be due to the few collections made so far in N.W. Mexico. Distribution : N.W.

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[1] *S. fendleri*, subsp. *arizonicum* Hawkes a subsp. *fendleri* corolla rotata acuminibus parviusculis lobisque brevibus antheris parvis 3 mm. longis differt.

[2] *S. hjertingii* Hawkes a *S. fendleri* A. Gray caule foliis pedunculo pedicellis calycibusque glabris vel glabriusculis, foliolis plerumque petiolulatis angustis, et corolla glabra differt.

Mexico, States of Durango and Zacatecas (also San Luis Potosí ?). Growing in dry oak-juniper scrub at 2,200-2,400 m. 2n = 48.

4. S. polytrichon Rydb. (Bull. Torr. Bot. Cl., **51**, 150, 1924)
S. macropilosum Corr. (Wrightia, **2**, 189-90, 1961)
S. wightianum Rydb. (Bull. Torr. Bot. Cl., **51**, 149, 1924)

Distinguished by the dense spreading pubescence of thick white hairs on the whole plant, and especially on the pedicel, both below and above the articulation; corolla generally white, occasionally mauve; articulation high. Some forms possess sparse leaf pubescence, but the spreading pedicel pubescence is a constant feature. Shade forms (one cultivated under glass) have been described by Correll as *S. macropilosum* and *S. wightianum*; these seem to be no more than phenotypic variants of *S. polytrichon*.

White-flowered forms known to breeders as "*S. boreale*" should probably be classed as *S. polytrichon* and not as *S. boreale* or *S. fendleri*. If the corolla is stellate, however, it is likely that they may belong to *S. jamesii* (series Pinnatisecta). Bitter's *S. boreale* (A. Gray) Bitt. was said to include white-flowered forms mentioned by A. Gray when describing *S. fendleri* and which Bitter himself had not seen. The name "boreale" is thus a *nomen dubium*, since there is no means of knowing what Gray had in mind when mentioning these white-flowered forms.

Distribution: Central and N.W. Mexico (Querétaro to Chihuahua and Nuevo León) in dry stony and shrubby places, occasionally as a weed of cultivation, at 2,000-2,400 m. 2n = 48.

5. S. stoloniferum Schlechtd. et Bché. (Linnaea, **8**, 255, 1833)
S. ajuscoense Buk. (*apud* Rybin, Bull. Appl. Bot., **20**, 699-700, 1929)
S. antipoviczii Buk. (*apud* Rybin, Bull. Appl. Bot., **20**, 700, 1929)
S. candelarianum Buk. (Bull. Appl. Bot. Genet. Plant Breed., Suppl. 47, 218, 1930)
S. longipedicellatum Bitt. (in Fedde, Repert., **11**, 457-58, 1912)
S. malinchense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 117, 1944)

S. neoantipoviczii Buk. (Bull. Appl. Bot. Genet. Plant Breed., Suppl. 47, 217, 1930)

S. tlaxcalense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 117-18, 1944)

A very polymorphic species, differing in degree of leaf dissection and flower colour (white to purple). Constant features are the circular corolla outline with large acumens, the coarse adpressed hairs over all green parts (not spreading as in *S. polytrichon*), the pedicel glabrous or only sparsely hairy above articulation, and the acuminate leaflets. Locally abundant forms (previously described as species) are found in certain regions (*e.g. S. antipoviczii* and *S. ajuscoense* in the higher regions and *S. longipedicellatum* in the lower parts of the Valley of Mexico ; *S. tlaxcalense* in the eastern part of the distribution range. Detailed studies are needed here to elucidate the pattern of variability. Distribution : Central Mexico from Toluca to Orizaba (north to Chihuahua ?). Dry plateaux, valleys, and hillsides, chiefly as ruderal plants, from 1,800-3,000 m. 2n = 48.

6. S. × vallis-mexici Juz. (Bull. Acad. Sci. U.R.S.S., **2**, 315-16, 1937)

This hybrid " species " is distinguished from *S. stoloniferum* by the dark purple corolla, and broadly obovate to rhomboid terminal leaflet which is larger than the laterals. Formed as a hybrid between *S. stoloniferum* (2n = 48) and *S. verrucosum* (2n = 24), occurring in the Valley of Mexico and elsewhere, where the altitude ranges of these two species overlap. Woods, fields, waysides, from 2,400-3,000 m. 2n = 36.

SERIES XIII *POLYADENIA* BUK.

(*ex* Correll, U.S. Dept. Agric. Monogr., No. 11, 127, 1952)

Tuber-bearing herbs with a very dense indumentum of glandular hairs of an objectionable odour ; most of these glands possess 2-celled stalks—a feature not known in any other tuber-bearing *Solanum* species. Corolla white, pentagonal to sub-stellate. Berries ovate, cordate or conical, somewhat flattened, with black streaks, especially on the edges. Distribution : Central to southern Mexico on dry stony hillsides or in damp rain forests, according to the species.

Key to species

All green parts provided with a very dense covering of many-celled non-glandular spreading hairs (as well as the numerous glands), easily visible to the naked eye ; stem purple-pigmented ; berry long-conical . **1. S. lesteri**

All green parts with very few non-glandular hairs of the type described above, and these are not easily visible to the naked eye ; stem unpigmented ; berry ovate to cordate **2. S. polyadenium**

1. S. lesteri [1] Hawkes & Hjerting, sp. nov.

Differs from *S. polyadenium* in the more robust habit, thick purple-pigmented stem, dense indumentum of long spreading multicellular hairs on all green parts, in addition to the glandular ones, and long-conical pointed 2-grooved and flattened berries. A distinct species, obviously related to *S. polyadenium*, but occurring under quite different ecological conditions. Distribution : Endemic to South Mexico (Oaxaca State), in damp mountain forests at 2,300 m., growing with *S. iopetalum*. 2n = 24.

2. S. polyadenium Greenm. (Proc. Amer. Acad. Arts & Sci., **39**, 89, 1904)

S. polyadenium subsp. *orizabae* Bitt. (in Fedde, Repert., **12**, 7-8, 1913)

Whole plant covered with very frequent, stalked glands ; stalks generally 2-celled. Very sparse multicellular non-glandular hairs also present but not easily visible without a lens. Whole plant more slender and less robust than *S. lesteri*. Corolla white, pentagonal. Bitter's subsp. *orizabae* does not differ very significantly from the type and in any case a certain amount of variation, chiefly in leaf dissection, exists in natural populations. Distribution : Central Mexico, from Vera Cruz to Jalisco ; on dry stony hillsides, by old walls, on old lava and amongst trees and shrubs, from 1,900-2,900 m. 2n = 24.

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[1] *S. lesteri* Hawkes & Hjerting a *S. polyadenium* Greenm. habitu robustiore, caule crasso purpureo-pigmentato, pilorum multicellularium acutorum patentium denso indumento in omnibus partibus viridibus, baccisque longis conicis acutis bisulcatis complanatis differt.

SERIES XIV *CUNEOALATA* HAWKES

(Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 118, 1944)

Small straggling tuberiferous herbs with pinnatifid leaf, the rhachis with narrow wedge-shaped decurrent wings between each pair of leaflets ; corolla purplish, sub-stellate to rotate with well delimited petal acumens. Geographical distribution : Central Bolivia to N.W. Argentina and N. Chile, in dry cactus deserts and scrub. Possibly drought-resistant.

1. S. infundibuliforme Phil. (Anal. Mus. Nac. Chile, 2nd ed. Bot., 65, 1891)

S. glanduliferum Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 118-19, 1944)

S. microphyllum Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 118, 1944 ; non *S. microphyllum* Dun., Hist. Solan., 187, 1813)

S. pinnatifidum Cárdenas (Rev. Agric., Cochabamba, **2**, 33-34, 1944 ; non *S. pinnatifidum* Ruiz et Pav., Flora Peruv., **2**, 37, 1798-1802)

S. platypterum Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 118, 1944)

S. xerophyllum Hawkes (J. Linn. Soc., Bot., **53**, 108, 1945)

Leaflets roughly lanceolate, linear-lanceolate to linear. Interjected leaflets entirely absent. Corolla pale mauve to purplish, occasionally white, in shape varying from sub-stellate to completely rotate (circular with well-marked acumens, as in series Longipedicellata). A form from the Argentine-Bolivian border previously classed as *S. platypterum* owing to the very wide rhachis wings is not sufficiently distinct to be given specific rank ; similarly with *S. glanduliferum* which bears some glands on the leaves, and *S. xerophyllum* which possesses narrow linear leaflets, due probably to very poor soil and moisture conditions. Distribution : Central Bolivia to N.W. Argentina and N. Chile ; dry cactus and scrub deserts at 2,450-4,100 m. 2n = 24.

SERIES XV *MEGISTACROLOBA* CARD. & HAWKES

(J. Linn. Soc. Bot., **53**, 93, 1945)

Rather short stemmed or straggling tuber-bearing herbs whose leaves bear a very enlarged terminal leaflet, with the lateral leaflets much smaller than the terminal or sometimes completely absent. The laterals when present are broadly decurrent on to the rhachis at the basiscopic side ; peduncle very short ; pedicel long, with very high articulation ; corolla sub-stellate to rotate, purple. Distribution : N. Peru to N.W. Argentina, growing in waste places, open mountain pastures, etc.

Key to species

1. Pedicels covered with dense long spreading pubescence 2
Pedicels sparsely pubescent ; hairs short, adpressed . 4
2. Leaf simple (Bolivia) . . . . . **12. S. ureyi**
Leaf with at least a few minute lobes (N. Peru) . 3
3. Lateral leaflets reduced to minute lobes ; corolla rotate **10. S. hastiforme**
Lateral leaflets in better-developed leaves at least $\frac{1}{3}$ to $\frac{1}{2}$ length of terminals ; corolla sub-stellate **8. S. chavinense**
4. Corolla fully rotate, with lobes well-developed and easily distinguishable from acumens 5
Corolla sub-stellate to pentagonal, the lobes gradually passing into the acumens 8
5. Leaf simple or with one or two lateral leaflets present in plants with long stem only . . **1. S. boliviense**
Lateral leaflets or lobes always present, even in very short-stemmed plants 6
6. Decurrent portions of lateral lobes or leaflets rather narrow and short . . . . . **4. S. raphanifolium**
Decurrent portions of lateral lobes or leaflets very broadly triangular, running down rhachis for a considerable way 7
7. Leaflets acute to acuminate ; interjected leaflets present **11. S. hawkesii**

Leaflets obtuse ; no interjected leaflets present **6. S. sogarandinum**

8\. Terminal leaflet and minute laterals (if present) markedly acuminate . . **5. S. sanctae-rosae**

Terminal leaflet and minute laterals (if present) obtuse or acute, never acuminate 9

9\. Leaf simple, never with more than one pair of minute lobes at base of blade 10

Leaf with well-developed lateral lobes or leaflets . 12

10\. Leaf oblong-elliptic, rather sharply truncate at base **9. S. ellipsifolium**

Leaf rhomboid, ovate or spathulate, cuneate at base . 11

11\. Leaf ± ovate to rhomboid . **3. S. megistacrolobum**

Leaf long-spathulate or very long obovate **7. S. toralapanum**

12\. Decurrent portions of lateral lobes very broadly triangular and long . . . . . **7. S. toralapanum**

Decurrent portions of lateral lobes or leaflets rather narrow and short 13

13\. Lateral leaf lobes about equal in size to the terminals, at least in the upper leaves . **2. S. × bruecheri**

Lateral leaf lobes markedly smaller than terminals . 14

14\. Terminal leaflet broadly ovate to orbicular **4. S. raphanifolium**

Terminal leaflet long ovate to obovate, long ellipsoid or rhomboid . . . . . **3. S. megistacrolobum**

1. S. boliviense Dun. (in DC. Prodr., **13**, I, 43, 1852)

A rosette or sometimes caulescent species, with generally completely simple leaves and rotate dark purple corolla. Distribution : Central Bolivia to N.W. Argentina ; dry bushy places and cultivated fields, from 2,600-3,650 m. 2n = 24.

2. S. × bruecheri Corr. (Wrightia, **2**, 176-77, 1961)

A naturally occurring hybrid, formed probably between *S. acaule* and *S. megistacrolobum* (see Brücher, 1959) ; some of Correll's specimens would seem to be hybrids of *S. infundibuliforme* × *S. megistacrolobum*, however (*Correll A.* 682). Distribution : N.W. Argentina, amongst rocks and stone walls, etc., from 3,500-3,700 m. n = 36 (*fide* Brücher).

3. S. megistacrolobum Bitt. (in Fedde, Repert., **10**, 536-37, 1912)

S. alticola Bitt. (in Fedde, Repert., **12**, 5-6, 1913)

S. tilcarense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 119-20, 1944)

Rosette-forming or with straggling stem; the terminal leaflet long ovate to obovate, long-ellipsoid or rhomboid, rounded or obtuse at apex (or with a minute mucron only); entire-leaved rosette forms of this species from N. Bolivia were described as *S. alticola*, whilst forms with more rhomboid terminal leaflet from N.W. Argentina were named *S. tilcarense*. Most of the differences may probably be ascribed to variations in habitat. Distribution: S. Peru to N.W. Argentina, high altitude plateaux and mountain slopes, from 2,600-4,300 m. 2n = 24.

4. S. raphanifolium Cárd. et Hawkes (J. Linn. Soc., Bot., **53**, 94-95, 1945)

Distinguished from *S. megistacrolobum* chiefly by the broadly ovate to orbicular terminal leaflet and the paler sub-stellate to rotate corolla. Distribution: S. Peru, waste places, hillsides, etc., from 2,800-3,800 m. 2n = 24.

5. S. sanctae-rosae Hawkes (Ann. Mag. Nat. Hist., Ser. 12, **7**, 702-03, 1954)

Distinguished from *S. megistacrolobum* and *S. raphanifolium* by the *acuminate* lateral and terminal leaflets, the small rosette habit, deep blue-purple corolla, with poorly marked acumens and large globose stigma. Distribution: N.W. Argentina, in high mountain pastures, sandy and rocky places, etc., from 2,500-3,800 m. 2n = 24.

6. S. sogarandinum Ochoa (Agronomía, Lima, **19**, 169-72, 1954)

Very closely related to *S. megistacrolobum*, of which it may perhaps represent a northern subspecies; differs chiefly in the very robust inflorescence and rotate (not sub-stellate) corolla. Distribution: N. Peru, páramos (high Andean grassland), at 3,550 m. 2n = 24.

7. S. toralapanum Cárd. et Hawkes (J. Linn. Soc., Bot., **53**, 98-99, 1945)

S. decurrentilobum Cárd. et Hawkes (J. Linn. Soc., Bot., **53**, 97-98, 1945)

Distinguished from *S. megistacrolobum* by the very broadly triangular decurrent rhachis wing, or in the simple leaved forms by the very long spathulate or long obovate leaf blade. Distribution : C. Bolivia, field margins, rocky and grassy slopes, etc., from 3,000-4,500 m. 2n = 24.

8. S. chavinense Corr. (Wrightia, **2**, 185-86, 1961)

A caulescent species with 1-2 pairs of lateral leaflets, densely pubescent pedicels and large showy stellate deep purple corolla. Distribution : N. Peru, amongst rocks, trees and shrubs at 3,500-4,200 m.

9. S. ellipsifolium Cárd. et Hawkes (J. Linn. Soc., Bot., **53**, 100-01, 1945)

Leaf simple, elliptic, with truncate base ; plant growing in a rosette. Distribution : C. Bolivia.

10. S. hastiforme Corr. (Wrightia, **2**, 187-88, 1961)

Lateral leaflets reduced to minute decurrent lobes at base of terminal ; leaf somewhat hastate ; pedicels covered with spreading hairs ; corolla lavender-purple, rotate, with well-marked lobes and distinct acumens. (Material not seen by me.) Distribution : N. Peru, along a bushy rocky stream, at 3,200 m.

11. S. hawkesii Cárd. (J. Linn. Soc., Bot., **53**, 95-96, 1945)

Distinguished from other species in this series by the tall stem, presence of interjected leaflets and more or less rotate corolla. May need to be separated from Megistacroloba after further study. Distribution : S. Peru. Damp forests at 2,000 m.

12. S. ureyi Cárd. (Bol. Soc. Peruana Bot., **5**, 32-33, 1956)

Leaves simple, obovate to spathulate ; stem, peduncles and pedicels thickly clothed with long spreading hairs ; corolla purple-violet, rotate, with well-developed lobes and distinct, rather small acumens. Possibly related to *S. toralapanum*, though differing in the dense pubescence and the rotate corolla. (Material not seen by me.) Distribution : Bolivia (Cochabamba) on wet grassy mountain slopes at 3,600 m.

SERIES XVI *INGAEFOLIA* OCHOA

(Sol. tuber. silv. Peru, Lima, 68, 1962 ; *ex* Correll, in Texas Res. Found. Contrib., **4**, 129, 1962)

Tuber-bearing herbs with erect or decumbent habit, thick winged stems, imparipinnate leaves with broadly winged rhachis, the wing continuing right to the leaf base, and rotate corolla. Distribution: Andes of northern Peru.

Key to species

Leaflets 1-3(-4)-paired; interjected leaflets absent; lateral leaflets sessile . . . . . **1. S. ingaefolium**

Leaflets 4-5-paired; interjected leaflets or lobes 0-5; primary lateral leaflets petiolulate **2. S. rachialatum**

1. S. ingaefolium Ochoa (Agronomía, Lima, **26**, 319-22, 1959)

A very curious and distinct species with leaves similar to those of the Leguminous genus *Inga*. Stem with broad wings; lateral leaflets acuminate, decurrent; rhachis with broad wings which swell out from the point of insertion of each leaflet pair and become slightly narrowed towards the next pair below; no interjected leaflets; corolla lilac, rotate. Distribution: Endemic to the humid mountain forests of N. Peru (Piura) at altitudes of 2,800-3,000 m.

2. S. rachialatum Ochoa (Agronomía, **19**, 172-74, 1954)

Differs from *S. ingaefolium* in possessing narrow stem wings, petiolulate lateral leaflets (4-5 pairs instead of 1-3(-4)), interjected leaflets or lobes projecting from the irregularly winged rhachis, white rotate corolla, etc. (Material not seen by me.) Distribution: Endemic to the (dry?) lower forest regions of N. Peru (Piura) at altitudes of 1,200-1,900 m.

SERIES XVII *TUBEROSA* RYDB.

(Bull. Torr. Bot. Cl., **51**, 146-48, 1924; Buk. & Kameraz, Bases of Potato Breeding, 18, 1959, *sensu stricto*)

Andigena Buk. (*ex* Buk. & Kameraz, Bases of Potato Breeding, 24, 1959)

Andreana Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, **50**, 1944, *nomen nudum*)

Minutifoliola Corr. (Texas Res. Found. Contrib., **4**, 216-18, 1962)

Transaequatorialia Buk. (*ex* Buk. & Kameraz, Bases of Potato Breeding, 21, 1959)

Vaviloviana Buk. (*ex* Buk. & Kameraz, Bases of Potato Breeding, 18, 1959)

This tuber-bearing series contains all the cultivated potato species as well as the wild and weed species most closely related to them. It is characterised by imparipinnate or simple leaves, bifurcate peduncle, rotate to semi-stellate corolla and round berries. Series *Tuberosa* is confined to the Andes of South America and to the adjacent coastal belt in temperate and subtropical latitudes. It spreads southwards from Venezuela through Colombia, Ecuador, Peru, Bolivia, N.W. Argentina and Chile as far as 45° south. The greatest concentration of species is in Peru, Bolivia and N.W, Argentina, and in this region a number of species occur whose boundaries are not very well defined and which still need further study. Although most *Tuberosa* species are diploid, some triploids, tetraploids and pentaploids also occur.

In addition to the species that are definitely considered to belong to series *Tuberosa* there are a number of insufficiently known species that may possibly need to be separated into distinct series when they have been studied in greater detail. These have been marked with an asterisk in the list which follows.

We shall deal with the wild species first, indicating where appropriate their possible connections with the cultivated ones.

The key to *Tuberosa*, given below, includes wild species only. A key to the cultivated species is given on p. 139. Presence of pink or red pigmentation in the flowers and/or tubers and a definite pigment pattern on the tubers are two indications of cultigens, though some escaped forms of *S. tuberosum* lack these features.

Key to wild species

(Key to cultivated species : p. 139)

1. Flowers white or nearly so 2
Flowers blue, purple, lilac, etc., at most with pale acumens or interpetalar portions 13
2. Anthers not clearly delimited from filaments, either in form or colour (Chile, W. Argentina) **15. S. maglia**
Anthers and filaments quite distinct 3
3. Leaf very rough and with undulate-crenulate margins; whole plant densely and coarsely pubescent (N. Peru) **36. S. cajamarcense**
Plant without this combination of characters . . . 4
4. Leaf simple or with not more than 1-2(-3) pairs of lateral leaflets which decrease in size rapidly towards the leaf base 5

Leaf with 4 or more pairs of lateral leaflets . . . 8

5\. Plant entirely glabrous ; calyx lobes oblong, leafy (Bolivia) **9. S. gandarillasii**

Plant with easily visible pubescence . . . 6

6\. Hairs very short, 3-celled, triangular, adpressed (Argentina) . . . . . . **29. S. venturii**

Hairs multicellular, large 7

7\. Corolla pentagonal to sub-stellate, completely white ; acumens 4 mm., flat (Argentina, Bolivia) **18. S. microdontum**

Corolla rotate, tinged lavender below ; acumens not more than 3 mm., hooded (N. Peru) **8. S. chiquidenum**

8\. Plant glabrous ; lateral leaflets narrow lanceolate, at least 5 times as long as broad, 6-9-paired (Peru) **11. S. gracilifrons**

Plant pubescent ; lateral leaflets less than 5 times as long as broad 9

9\. Whole plant covered with a dense soft velvety pubescence of thin non-gladular hairs (also some glands) ; stem woody (S. Peru) **14. S. lignicaule**

Not as above 10

10\. Articulation in lower third of pedicel or near base ; leaf margins with thick adpressed hairs on swollen base (Argentina) . . . . . **12. S. kurtzianum**

Articulation at centre or above 11

11\. Leaflets sessile ; interjected leaflets orbicular-cordate (N. Peru) . . . . . **45. S. mochicense**

Leaflets subsessile to petiolulate ; interjected leaflets ovate to lanceolate, petiolulate 12

12\. Leaf 5-6-jugate ; lateral leaflets subsessile to petiolulate, narrow lanceolate ; corolla substellate **24. S. × setulosistylum**

Leaf 2-4-jugate ; lateral leaflets petiolulate, elliptic-oblong ; corolla rotate to substellate . . **23. S. rechei**

13\. Plants densely glandular-pubescent 14

Plants with normal hairs and not more than a few glands 15

14\. Corolla substellate ; leaflets petiolulate, not acuminate (Bolivia) . . . . . **4. S. berthaultii**

Corolla rotate ; leaflets sessile, acuminate (Coastal region of central Peru) . . . . **32. S. wittmackii**

15\. Lateral leaflets 0-2(-3) paired, decreasing rapidly towards base of leaf 16
Lateral leaflets 3-6-paired, at least two pairs being as large as or larger than the terminal 28
16\. Margins of corolla lobes rolled inwards ; berries verrucose, with raised white spots (Mexico)
(See **Demissa. S. verrucosum** p. 121)
Margins of corolla lobes not rolled inwards ; berry without raised white spots (S. America) . . . 17
17\. Upper lateral leaflets very widely decurrent on to rhachis 18
Upper lateral leaflets not or only slightly decurrent on to rhachis 19
18\. Corolla substellate ; calyx acumens short, with short adpressed pubescence (See **Megistacroloba**, p. 128)
Corolla rotate ; calyx acumens linear-spathulate, with spreading hairs (S. Peru) . . **53. S. sandemanii**
19\. Lateral leaflets petiolulate 20
Lateral leaflets sessile to subsessile 23
20\. Leaflets softly pubescent below (Bolivia)
55. S. torrecillasense
Leaflets not softly pubescent below 21
21\. Leaflets markedly acuminate . . **3. S. andreanum**
Leaflets not acuminate, obtuse 22
22\. Leaf 1-2-jugate ; pedicel weakly pubescent
17. S. medians
Leaf 2-3-jugate ; pedicel strongly pubescent
57. S. weberbaueri
23\. Corolla large, 4 cm. diam. or more 24
Corolla medium-sized, about 3 cm. diam. 25
24\. Lateral leaflets at least twice as long as broad
52. S. rhomboideilanceolatum
Lateral leaflets 1-1·5 times as long as broad
40. S. huanucense
25\. Leaves in a basal rosette ; stem very short
50. S. pumilum
Leaves spread along the stem 26
26\. Upper laterals as large as the terminal leaflet **2. S. alandiae**
Upper laterals about $\frac{1}{2}$ to $\frac{2}{3}$ the terminal leaflet . 27
27\. Stem short ; leaves less than 4 cm. long.
38. S. colominense
Stem medium-lengthed ; leaves more than 4 cm. long
56. S. virgultorum

28. Leaf completely glabrous 29

Leaf with some hairs at least 32

29. Leaflets about 4 times as long as broad **1. S. acroscopicum**

Leaflets about twice as long as broad 30

30. Lateral leaflets 4-5-paired, clearly petiolulate (Bolivia) **39. S. doddsii**

Lateral leaflets 3-(4-) paired, sessile 31

31. Leaflets apically obtuse (Peru) **41. S. huarochiriense**

Leaflets apically acute to acuminate (Ecuador) **54. S. suffrutescens**

32. Corolla sub-stellate, *i.e.* the length of each lobe about equal to the breadth, and the "shoulders" poorly developed 33

Corolla pentagonal or rotate, the lobes having distinct shoulders and well-differentiated acumens . . 43

33. Pedicel articulation very high; terminal leaflet much larger than laterals . (See **Megistracroloba,** p. 128)

Plants not possessing the above characteristics . . 34

34. Stigma very small, not or hardly thicker than style apex **21. S. oplocense**

Stigma larger than style apex 35

35. Corolla fairly large (more than 3·5 cm. diam.) deep purple; calyx very dark purple 36

Corolla medium-sized, lavender or medium purple; calyx green or only slightly pigmented 37

36. Upper lateral leaflets more than 2½ times as long as broad **42. S. liriunianum**

Upper lateral leaflets 2½ times as long as broad, or less **30. S. vernei**

37. Leaf provided with a very large number (about 12 or more pairs) of sessile interjected leaflets (Ecuador) **44. S. minutifoliolum**

Interjected leaflets few or none; if frequent, then petiolulate 38

38. Lateral leaflets at least 3 times as long as broad . . 39

Lateral leaflets about 2-2½ times as long as broad . 41

39. Lateral leaflets 3(-4)-paired; interjected leaflets normally absent . . . . . . **31. S. vidaurrei**

Lateral leaflets (4-)5-6-paired; interjected leaflets normally quite frequent 40

40\. All leaflets with long petiolules **24. S. × setulosistylum**
Upper lateral leaflets generally sessile or subsessile and decurrent . . . . . **26. S. spegazzinii**

41\. Interjected leaflets absent (Ecuador, N. Peru) **51. S. regularifolium**
Interjected leaflets present, at least in the better-developed leaves 42

42\. Lateral leaflets about 2½ times as long as broad; a low-growing wild species (Argentina) **10. S. gourlayi**
Lateral leaflets about twice as long as broad; a robust weed species (Bolivia) . . **28. S. sucrense**

43\. Stem, peduncle and pedicels with rather dense long spreading hairs 44
Not as above; hairs short and/or adpressed . . 46

44\. Leaf (4-)5-8-jugate, with numerous interjected leaflets **19. S. multidissectum**
Leaf 3-4(-5)-jugate; interjected leaflets sparse, 2-3-(5) paired 45

45\. Low-growing rosette plant with very short stem, not very pilose (Colombia) . . **43. S. lobbianum**
Tall upright plant with long stem, markedly pilose throughout . . . . **33. S. amabile**

46\. Calyx bilabiate with sepals in groups of 2 or 3 . . 47
Calyx regular, the sepals not in groups 48

47\. Flowers large, 3-4 cm. diam., with oblong corolla lobes **25. S. soukupii**
Flowers medium-sized (up to 3 cm. diam.); corolla lobes broadly triangular, sloping **27. S. sparsipilum** (in part)

48\. Pedicel articulation below centre, sometimes quite close to base; corolla white and red-purple **12. S. kurtzianum**
Pedicel articulation at or above centre; corolla with no white interpetalar portions 49

49\. Upper lateral leaflets more than 2½ times as long as broad 50
Upper lateral leaflets 2½ times as long as broad or less 56

50\. Leaves 3-4-jugate, shining and glabrescent above, densely pubescent below; interjected leaflets 0-2-paired (Peru) **16. S. marinasense**
Leaves pubescent on both surfaces 51

51\. Calyx acumens not more than 1·5 mm. long . . 52
Calyx acumens 2-4 mm. long 53

52. Leaf very sparsely pubescent ; leaflets long oblong in shape . . . . **46. S. mollepujroense**
Leaf with frequent coarse hairs ; leaflets lanceolate to narrow lanceolate . . . **13. S. leptophyes**

53. Largest lateral leaflets 6-7 cm. long 54
Largest lateral leaflets to 4·5 cm. long 55

54. Interjected leaflets numerous, at least 10 pairs in the better-developed leaves (N. Bolivia) **7. S. candolleanum**
Interjected leaflets sparse, 3-4-paired (N. Peru) **48. S. orophilum**

55. Leaf rather sparsely pubescent above ; interjected leaflets sparse . . . . **22. S. pampasense**
Leaf densely covered above and below with adpressed silky pubescence ; interjected leaflets numerous **6. S. canasense**

56. No interjected leaflets present in any leaf ; calyx glabrous (Venezuela) . . . **49. S. paramoense**
Interjected leaflets always present in the better-developed leaves ; calyx pubescent (Peru, Bolivia) . . 57

57. Interjected leaflets numerous ; from 5 to 14 pairs per leaf in the better developed leaves 58
Interjected leaflets sparse, 0-4(-5) pairs per leaf . 60

58. Lower surface of leaf densely white-velvety pubescent ; corolla bright sky-blue . **37. S. coelestipetalum**
Lower leaf surface not densely white-velvety pubescent ; corolla lavender to purple 59

59. Pedicels densely yellow-velvety pubescent ; hairs rather short ; calyx densely pubescent . **47. S. ochoae**
Pedicels with short ± adpressed hairs ; calyx very sparsely pubescent . . . . **20. S. multiinterruptum**

60. Calyx acumens long, 1·5-3 mm. . **34. S. ambosinum**
Calyx acumens short, 0·5-1 mm. 61

61. Habit short, semi-rosette ; leaflets 2·5 times as long as broad . . . . . . **5. S. bukasovii**
Habit much more vigorous ; leaflets about twice as long as broad 62

62. Corolla rotate, dark purple, with free parts of lobes only about 4 mm. long . . . **35. S. brevicaule**
Corolla pentagonal-rotate, medium purple, with free parts of the lobes 8-10 mm. long . **27. S. sparsipilum**

Key to cultivated species

1\. Articulation of pedicel high, 2-4(-6) mm. below calyx base, always more than ¾ length of pedicel ; leaves stiff, not arched at tip 2

Articulation lower, not more than ⅔ length of pedicel, sometimes at or below centre ; leaves often slightly arched at tip 4

2\. Corolla roughly pentagonal in outline (not completely rotate) ; upper lateral leaflets broadly decurrent on to rhachis ; leaves softly hairy . **58. S. ajanhuiri**

Corolla rotate in outline, the lobes very short ; upper lateral leaflets not (or only barely) decurrent on to rhachis ; leaves not softly hairy 3

3\. Pedicels indistinctly articulated ; corolla blue, not more than 2·5 cm. diam. ; common peduncle short, 2-4 cm. long . . . . **61. S. × juzepczukii**

Pedicels distinctly articulated ; corolla purple, 3-3·5 cm. diam. ; common peduncle longer, 5-10 cm. or more long . . . . . **60. S. × curtilobum**

4\. Calyx lobes short, oblong or short ovate-triangular, generally regularly arranged . . . **64. S. tuberosum**

Calyx lobes long-ovate, generally arranged irregularly (in 2 + 3, or 2 + 2 + 1 groups) 5

5\. Lobes of corolla 3 times as broad as long, generally broader than the corolla radius . . **59. S. × chaucha**

Lobes of corolla less than or only just as broad as long 6

6\. Leaf sparsely pubescent, shining in the living state ; tubers yielding in 3-4 months under 12-hour days and with no dormancy period . . . . **62. S. phureja**

Leaf more densely pubescent ; not shining in the living state ; tubers yielding in 5-6 months (or longer) under 12-hour days and with definite dormancy period **63. S. stenotomum**

Wild species

1.* S. acroscopicum Ochoa (Agronomía, Lima, **18**, 130-32, 1953)

Distinguished by the completely glabrous leaf, narrow lanceolate petiolulate leaflets and rich purple large showy corolla ; berry ellipsoid. Possibly related to series Conicibaccata and Piurana. Distribution : S. Peru (Tacna, Moquegua), in mountain forests (?) at 3,200-3,450 m. 2n = 48 (U.S.D.A. Bull. 533).

2. S. alandiae Córd. (Bol. Soc. Peruana Bot., **5**, 11-12, 1956)

Lateral leaflets 1-3-paired, decreasing rapidly in size from apex to base of leaf ; no interjected leaflets ; dense coarse pubescence ; corolla blue-lilac. Related to *S. microdontum*, and possibly derived from it by hybridization. Distribution : Bolivia (Cochabamba), amongst bushes on the high slopes of the Andes at 3,200 m.

3. S. andreanum Baker (J. Linn. Soc., **20**, 498-99, 1884)

S. pichinchense Bitt. et Sodiro (in Fedde, Repert., **10**, 533-34, 1912)

Characterized by 2-3 pairs of acuminate leaflets and purple rotate corolla. Distribution : S Colombia, N. Ecuador. Damp high altitude woods and bushy places at 2,200-2,900 m. 2n = 24.

4. S. × berthaultii Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 122, 1944)

S. vallegrandense Córd. (Bol. Soc. Peruana Bot., **5**, 23-25, 1956)

Very glandular species with pale violet-blue pentagonal to sub-stellate corolla. Almost certainly formed as a natural hybrid between *S. tarijense* (Commersoniana) and a blue-flowered mountain species, possibly *S. sparsipilum*. Distribution : Bolivia, eastern slopes of Andes in rather dry valleys amongst bushes and in waste places from 2,100-2,700 m. 2n = 24.

5. S. bukasovii Juz. (Bull. Acad. Sci. U.R.S.S., **2**, 303, 1937)

Low semi-rosette plants with delicate growth, 3-4-jugate leaves and 0-3(-5) pairs of interjected leaflets ; sparingly pubescent on all green parts. Flowers purple. Possibly related to *S. multidissectum* and *S. leptophyes*. Distribution : C. Peru, in the puna formation (high mountain pastures) at 3,000-3,900 m. 2n = 24.

6. S. canasense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 123, 1944)

S. lechnoviczii Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 124-25, 1944)

Closely related to *S. leptophyes*, from which it differs in the large rotate corolla, highly dissected leaves and the soft adpressed silky pubescence. Leaflets narrow, lanceolate; interjected leaflets numerous. Flowers blue-purple. Distribution: S. Peru. Dry stony places, often amongst bushes, at 3,200-4,000 m. 2n = 24.

7. S. candolleanum Berth. (Ann. Sci. Agron., Paris, **2**, 185, 1911)

S. mandonii A.DC. (Arch. Sci. Phys. Nat., **15**, 438, 1886; non *S. mandonis* Heurk et Muell. Arg. in Heurck, Obs. Bot., **78**, 1870)

Leaf highly dissected, with 5-6 pairs of narrow lateral leaflets and numerous interjected leaflets; calyx lobes lanceolate; acumens 2-4 mm. long; corolla purple. Distribution: N. Bolivia, dept. La Paz, on rocky mountain slopes, at 2,700-3,500 m. 2n = 24.

8. * S. chiquidenum Ochoa (Biota, **1**, 5-7, 1954)

Leaves with 1-2 pairs of lateral leaflets, decreasing in size rapidly towards leaf base; no interjected leaflets; coarse shining hairs on both surfaces; calyx sub-glabrous, with linear acumens; corolla white, tinged with lavender, rotate. Bears some resemblance to *S. microdontum*, but may not be very closely related to it. Distribution: N. Peru, amongst bushes and in grass, at 2,800-3,400 m.

9.* S. gandarillasii Cárd. (Bol. Soc. Peruana Bot., **5**, 16-20, 1956)

A very distinct species, entirely glabrous, with enlarged terminal and few, rapidly decreasing, laterals; flowers small; calyx with oblong-spathulate, leafy lobes; corolla white. Distribution: C. Bolivia, eastern Andes, in dry cactus and scrub regions from 2,000-3,000 m. 2n = 24. (Ross.)

10. S. gourlayi Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 120-21, 1944)

Small rosette or semi-rosette plants with ovate-lanceolate to oblong-lanceolate leaflets which are often slightly decurrent; terminal leaflet broader than laterals; flowers pale purple, semi-stellate. Distribution: N.W. Argentina. Dry hillsides amongst cactus and scrub vegetation at 2,600-4,000 m. 2n = 24.

11.* S. gracilifrons Bitt. (Beibl. Bot. Jahrb., No. 119, **54**, 6-7, 1917)

Distinguished by the glabrous very numerous, narrow leaflets at least 5 times as long as broad and white corolla. Possibly related to series Piurana. Distribution: C. Peru, dept. Huancavelica. Dry cactus and scrub vegetation at 1,900-2,000 m. 2n = 24.

12. S. kurtzianum Bitt. et Wittm. (Bot. Jahrb., **50**, Suppl., 548-50, 1914)

S. macolae Buk. (Rev. Argent. Agron., **4**, 239-40, 1937)

S. velascanum Bitt. et. Wittm. (Bot. Jahrb., **50**, Suppl., 551-52, 1914)

Distinguished by the elliptic-obtuse to oblong leaflets with well-marked marginal hairs set on cushions of tissue and visible without a lens; also by the very low pedicel articulation placed in the lower third. Flowers to rotate to sub-stellate, white or with central petal streak of bright violet on external surface only. Distribution: W. Argentina (provs. Mendoza to Catamarca) on dry bushy hillsides, etc., from 1,400-3,000 m. 2n = 24.

13. S. leptophyes Bitt. (in Fedde, Repert., **12**, 448-49. 1913)

S. pachytrichum Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 121-22, 1944)

A low-growing slender species with narrow-lanceolate leaflets 3-4 times as long as broad. Corolla pentagonal to rotate, purple. Leaf dissection and pubescence not as intense generally as with *S. canasense*. *S. leptophyes* is probably related to *S. bukasovii*, *S. canasense* and *S. spegazzinii*. Is is morphologically similar to some forms of the cultivated species *S. stenototum*, with which it may also perhaps have some affinities. Distribution : South Peru, north Bolivia. Dry open places or amongst scrub from 2,500-4,000 m. 2n = 24.

14.* S. lignicaule Vargas (Rev. Argent. Agron., **10**, 398, 1943)

S. vargasii Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 113, 1944)

Stem terete, somewhat woody, with velvety pubescence ; leaf softly pubescent, yellow-green. Corolla creamy white. A very distinct species of unknown affinities. Distribution : South Peru, dept. Cuzco, on dry bushy slopes and amongst stones at 3,000-3,500 m. 2n = 24.

15. S. maglia Schlechtd. (Hort. Halensis, **1**, 6, 1841)

S. collinum Dun. (in DC. Prodr., **13**, I, 36, 1852)

A large bushy plant with (1)-2-3-paired broadly ovate leaflets, and broader terminal leaflet. Corolla white, rotate. Stamens very characteristic, in a loose-barrel-shaped column ; anthers and filaments not well demarcated either in colour or form. Distribution : Central Chile, in the region of Valparaiso, near the sea coast to 120 m. ; Argentina, prov. Mendoza, in dry valleys at 1,500 m. 2n = 24, 36.

16.* S. marinasense Vargas (Papas Sudperuanas, Cuzco, **2**, 53, 1956)

S. cuzcoense Ochoa (Agronomía, **26**, 219, 1959)

Distinguished by the leaves which are bright glabrescent and shining above, paler and dull below ; 2-3 pairs of broadly lanceolate leaflets. Flower blue, very showy. A very distinct species, related to series Piurana. Distribution : S. Peru. Dry grassy hillsides from 2,000-3,500 m. 2n = 24.

17. S. medians Bitt. (in Fedde, Repert., **11**, 366-67, 1912)

S. neoweberbaueri Wittm. (Bot. Jahrb., **50**, Suppl., 540-48, 1914)

Low-growing straggling plants with enlarged terminal and smaller lateral leaflets in 1-2 pairs with sometimes 1-2 pairs of interjected leaflets. Distinguished from *S. microdontum* by the rhomboid terminal leaflet and from *S. raphanifolium* by the non-decurrent laterals. From *S. megistacrolobum* it is distinguished by the rotate corolla and linear calyx acumens. The forms with 36 chromosomes possess almost orbicular leaves and 0-1 pairs of interjecteds, whilst the diploids possess narrower leaflets and more laterals ; it does not seem really practicable to try to separate *S. neoweberbaueri* from *S. medians*. Distribution : C. Peru, coastal belt and mountains, in dry desert or scrub vegetation from sea level to 4,000 m. 2n = 24, 36.

18. S. microdontum Bitt. (in Fedde, Repert., **10**, 535-36, 1912 ; *emend.* Hawkes et Hjerting, Phyton, **9**, 144-45, 1960)

S. bijugum Bitt. (in Fedde, Repert., **10**, 533, 1912)
S. cevallos-tovari Cárd. (Bol. Soc. Peruana Bot., **5**, 13-15, 1956)
S. higueranum Cárd. (Bol. Soc. Peruana Bot., **5**, 20-21, 1956)

Large plants with winged stems and large simple to 2(-3)-jugate leaves, the terminal generally much larger than the laterals ; calyx acumens linear, unequal ; corolla white, substellate to pentagonal ; pubescence coarse, shining, of frequent multicellular hairs.

Subspecies microdontum. More slender than subsp. *gigantophyllum*, with narrow straight stem wings (0-2 mm. wide) and terminal leaflets rarely more than 8 cm. long.

Subspecies gigantophyllum (Bitter) Hawkes et Hjerting (Phyton, **9**, 144-45, 1960)

S. gigantophyllum Bitt. (in Fedde, Repert., **11**, 368-69, 1912)
S. simplicifolium Bitt. (in Fedde, Repert., **11**, 369-70, 1912)
S. simplicifolium Bitt. subsp. *gigantophyllum* Bitt. (in Fedde, Repert., **12**, 445, 1913)

Stem more robust, 3-20 mm. diam. ; wings 2-5 mm. wide, undulate and crenulate marginally ; terminal leaflet 8-18 cm. long.

Distribution : Subsp. *microdontum* : Central to southern Bolivia and north-west Argentina (Jujuy, Salta).

Subsp. *gigantophyllum* : North-west Argentina, southwards to Catamarca.

Both subspecies grow in high mountain rain forest on the eastern slopes of the Andes, from 1,000-3,000 m. 2n = 24.

19. S. multidissectum Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 124, 1944)

Low straggling herbs with generally highly dissected leaf and numerous interjected leaflets. Leaflets broadly ovate, the terminal subrotund. Long spreading hairs occur on the stem, rhachis and petiolules. Flower fairly large, pale blue. Differs from *S. leptophyes* and *S. canasense* in the wider leaflets and long spreading hairs.

Subspecies multidissectum. Differs from subsp. *neohawkesii* in lacking a true basal rosette in the young stage, and possesses ovate, rather than oblong leaflets. As one progresses northwards the leaf dissection decreases, so intergrading with subsp. *neohawkesii*.

Subspecies neohawkesii (Ochoa) Hawkes, comb. nov.

S. neohawkesii Ochoa (Rev. Argent. Agron., **19**, 231-34, 1952)

Plant forming a basal rosette at first ; leaf not quite so well-dissected as subsp. *multidissectum*.

Distribution : Subspecies *multidissectum* : South Peru.
Subspecies *neohawkesii* : Central Peru.

Both subspecies grow in high Andean pastures, amongst stones, by paths, etc., at altitudes of 3,300-4,100 m. 2n = 24.

20. S. multiinterruptum Bitt. (in Fedde, Repert., **12**, 56-57, 1913)

Leaflets sessile to subsessile ; 4-5 pairs of laterals which are about twice as long as broad, 5-14 pairs of interjected leaflets ; corolla very large, up to 5 cm. diam. Distribution : C. Peru, in high mountain grasslands, rocky slopes and among bushes, etc., at 3,000-4,000 m.

21. S. oplocense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 119, 1944)

S. subandigenum Hawkes var. *camarguense* Cárd. (Bol. Soc. Peruana Bot., **5**, 25-26, 1956)

Leaf 3-4-jugate with petiolulate but decurrent leaflets and denticulate margin ; corolla violet to purple, pentagonal to substellate ; anthers strongly tapered from base to apex, often 4-lobed at base ; stigma minute (thicker in tetraploid forms), generally not thicker than style apex. Distribution : S. Bolivia, N.W. Argentina on dry hillsides amongst stones, in cactus and scrub vegetation, at altitudes of 2,800-3,500 m. 2n = 24, 48. Little is yet known about the nature of the tetraploid races of this species.

22. S. pampasense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 125, 1944)

S. longimucronatum Vargas (Papas Sudperuanas, Cuzco, **2**, 60-61, 1956)

Leaflets lanceolate, covered with hairs of varying lengths, some gland-tipped ; calyx acumens linear, 2-4 mm. long ; corolla pale purple to pale blue, showy ; anthers long and narrow. Distribution : Central to south Peru (depts. Ayacucho, Apurímac) in dry subtropical interandine valleys at 2,000-2,900 m. (*Note.*—from reading the description of *S. pampasense* f. *glabrescens* Corr. (Wrightia, **2**, 183, 1961) I am very doubtful whether that taxon should be included with *S. pampasense.*) 2n = 24.

23. S. rechei [1] Hawkes et Hjerting, sp. nov.

Leaf 2-4-jugate lateral leaflets petiolulate, elliptic-oblong ; interjected leaflets generally few ; calyx acumens long, linear, 3-5 mm. long ; corolla white, rotate-pentagonal or substellate, about 3 cm. diam. ; anthers long narrow, about 7 mm. long. Related to *S. maglia* (and may be ancestral to that species), differing in the strongly petiolulate leaflets, very long calyx acumens, and long anthers clearly delimited from the filaments. Distribution : Argentina, endemic to prov. La Rioja, in dry valleys in and around Sierra Famatina, at about 1,100 m.

24. S. × setulosistylum Bitt. (in Fedde, Repert., **12**, 450-52, 1913)

S. puberulofructum Corr. (Wrightia, **2**, 193-94, 1961)

Vegetatively intermediate between *S. chacoense* and *S. spegazzinii*, but with corolla varying from white-stellate to

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[1] *S. rechei* Hawkes et Hjerting, *S. maglia* Schlechtd. affine est, sed foliis valde petiolulatis, acuminibus calycis longissimis, antheris ab filamentis manifeste delimitatis differt. Corolla alba, rotato-pentagonalis vel substellata ; antherae 7 mm. longae.

mauve-stellate or substellate. Style setae sometimes present. Leaf often highly dissected, with numerous narrow-ovate interjected leaflets. Young fruits sometimes puberulent. This name has been given to hybrid populations derived apparently from natural crosses between *S. chacoense* and *S. spegazzinii* Since the F_1 hybrids are fertile the variation in these populations is quite extensive. Distribution : N.W. Argentina in scrub and dry stony lands, waysides, etc., at 1,600-2,100 m. $2n = 24$.

25. S. soukupii Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 122-23, 1944)

S. espinarense Vargas (Papas Sudperuanas, Cuzco, **2**, 60, 1956)

Rather similar to *S. leptophyes* and *S. canasense* in habit, with small leaves and narrowly lanceolate leaflets. Differs, however, in the very large flowers, 3-4·5 cm. diam., and rounded quadrate corolla lobes with rather small acumen. May possibly be a derivative of *S. leptophyes* or *S. canasense*. Distribution : South Peru (Depts. Puno, Cuzco). Waste places and scrub-covered hillsides at 3,800-4,500 m. $2n = 24$.

26. S. spegazzinii Bitt. (in Fedde, Repert., **12**, 449-50, 1913)

S. famatinae Bitt. et Wittm. (Bot. Jahrb., **50**, Suppl., 552-53, 1914)
S. sleumeri Corr. (Wrightia, **2**, 195-96, 1961)

A widespread and phenotypically highly variable species connected to the Bolivian *S. leptophyes* and *S. pachytrichum* by means of the intermediate species *S. vidaurrei*. Leaflets long-elliptic, narrowing to each end, often decurrent ; interjected leaflets narrow ; corolla medium purple to lilac, substellate to pentagonal. Distribution : N.W. Argentina (south to La Rioja and San Juan provinces) in dry places in the interandine valleys and basins, from 1,900-3,100 m. $2n = 24$.

27. S. sparsipilum (Bitt.) Juz. et Buk. (in Vavilov, Theor. Bases Plant Breed., **3**, 11, 1937)

S. tuberosum L. subsp. *sparsipilum* Bitt. (in Fedde, Repert., **12**, 152-53, 1913)

S. abbottianum Juz. (Bull. Acad. Sci. U.R.S.S., **2**, 305-06, 1937)

S. anomalocalyx Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 126-7, 1944)

S. brevimucronatum Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 127, 1944)

S. calcense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 128-29, 1944)

S. catarthrum Juz. (Bull. Acad. Sci. U.R.S.S., **2**, 307-08, 1937)

S. fragariaefructum Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 129, 1944)

S. lapazense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 127-28, 1944)

S. membranaceum Vargas (Papas Sudperuanas, Cuzco, **2**, 62, 1956)

S. punoense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 123, 1944)

A very polymorphic species found as a weed of cultivated fields and waste places, morphologically very similar to *S. tuberosum* subsp. *andigena* (see below). Distinguished from that species, however, by the smaller more straggling habit, 2-4-jugate leaves with fewer interjected leaflets and rather smaller flower. Its wide distribution may be due to the fact that it was carried by man as a weed with the cultivated species all through Bolivia and Peru. The wide range of variability induced both Juzepczuk and myself to split it into several distinct species. Recent studies (unpublished) have shown, however, that all collections so far worked on are completely interfertile, showing no loss of fertility or viability even in the F_2 generation, and therefore all probably conspecific. *S. sparsipilum* may well have played an important role in the evolution of some of the cultivated potato species (Hawkes, 1956). Detailed field studies are needed to elucidate the complex pattern of variability of this species and to see whether it may be acquiring genes by natural hybridisation with other wild species in various parts of its geographical range. Distribution : Central Peru, southwards to Central Bolivia. Cultivated fields, waysides and waste places, from about 2,500-4,500 m. $2n = 24$.

28. S. sucrense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 126, 1944)

This weed and ruderal species is very similar vegetatively to forms of *S. tuberosum* subsp. *andigena*. It differs chiefly from these in the sub-stellate corolla with very long poorly delimited acumens and small calyx, anthers and style. Further studies are needed to elucidate its taxonomic position, though it seems to possess very close affinities with *S. tuberosum*. Distribution : Central Bolivia (depts. Chuquisaca, Potosí). An arable and garden weed, also found in waste places, from 2,500-3,900 m. 2n = 48.

29. S. venturii Hawkes et Hjerting (Phyton, **9**, 140-44, 1960)

Leaf with large terminal and smaller 1-3-paired laterals, occasionally simple, with very sparse closely adpressed short 3-celled triangular hairs, visible under a lens only ; calyx glabrescent or with a few hairs of same type as leaf hairs : corolla white, rotate to substellate. Related to *S. microdontum* but easily distinguished by the very characteristic pubescence. Distribution : Endemic to N.W. Argentina (provs. Tucumán, Catamarca) in high altitude grasslands (pajonales), at 2,000-2,800 m. 2n = 24.

30. S. vernei Bitt. et Wittm. (Bot. Jahrb., **50**, Suppl., 550-51, 1914)

A tall robust plant with large leaves and 4-6 pairs of ovate or ovate-lanceolate leaflets covered below with a white cottony or woolly pubescence. Flowers deep purple, often very large.

Subspecies vernei. Distinguished from subsp. *ballsii* by the apically acuminate petiolulate leaflets, acute ovate interjected leaflets and larger corolla.

Subspecies ballsii (Hawkes) Hawkes et Hjerting, comb. nov.

S. ballsii Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 121, 1944)

Leaflets generally sessile, acute to obtuse apically ; interjected leaflets generally shorter, obtuse and sessile ; corolla to 3 cm. diam.

Distribution : Subsp. *vernei* : N.W. Argentina, provs. Tucumán and Catamarca. Subsp. *ballsii* : N.W. Argentina, provs. Jujuy and Salta. Both occur in high-rainfall cloud forest in semi-open habitats (contrast *S. microdontum*) at 2,200-3,450 m. 2n = 24.

31. S. vidaurrei Cárd. (Bol. Soc. Peruana Bot., **5**, 26-30, 1956)

A delicate species with 3 (-4) pairs of lateral leaflets and no (occasionally 1-2 pairs) interjected leaflets ; leaflets narrow lanceolate, all pale yellowish-green, and with rather frequent coarse hairs ; corolla pentagonal, blue-violet. Seems to have affinities with *S. spegazzinii* and *S. leptophyes*. Distribution : S. Bolivia, N.W. Argentina, in high altitude, fairly damp grassland, at about 2,700-3,500 m. 2n = 24. (Ross.)

32. S. wittmackii Bitt. (in Fedde, Repert., **12**, 54-56, 1913)

S. vavilovii Juz. et Buk. (Bull. Acad. Sci. U.R.S.S., **2**, 302-03, 1937)

A wild species with generally a fairly dense glandular pubescence, 6-7 pairs of lanceolate acuminate lateral leaflets and numerous interjected leaflets ; calyx acumens linear or spathulate, corolla pale lilac, showy. Material from different collections differs considerably in the amount of glandular pubescence. In a variety described by Bitter (v. *glauciviride*) it is almost absent, whilst in the material of Vavilov (*S. vavilovii*) it is very dense. Distribution : Central Peru, near Lima. Desert coastal hills (lomas) vegetating only during the season of sea mists (garruas) during the months of July to September. 2n = 24.

Note.—A collection of this species formerly reported by Bukasov to be tetraploid, was in fact wrongly identified, according to Bukasov (verbal communication), and should possibly have been "*S. neoweberbaueri*".

33. S. amabile Vargas (Papas Sudperuanas, Cuzco, **2**, 58, 1956)

A tall-growing species with dense long spreading hairs on stem, peduncle and pedicels, 3-4-jugate leaves, and very large bright lilac to purplish corolla, 3.5-5 cm. diam. (Material not seen by me.) Distribution : C. to S. Peru on shrubby mountain slopes, at 2,500-3,700 m.

34. S. ambosinum Ochoa (Biota, Lima, **1**, 7-10, 1954)

Leaf 4-5-jugate, with few interjected leaflets and short hairs on all green parts; calyx acumens long, 1.5-3 mm.; corolla purple, rotate. (Material not seen by me.) Distribution: C. Peru, on shrubby mountain slopes at 2,200-2,500 m.

35. S. brevicaule Bitt. (in Fedde, Repert., **11**, 390-91, 1912)

A low-growing bushy species with 2-3(-4)-jugate lateral and few interjected leaflets, decurrent wings from leaf bases and small purple corolla. Distribution: C. Bolivia, dept. Cochabamba, amongst grass and shrubs, at 2,700-4,000 m.

36. S. cajamarcense Ochoa (Agronomía, Lima, **26**, 314-15, 1959; as *S. cajamarquense*)

A very distinctive species, the whole plant possessing a dense coarse pubescence; leaf rough, with undulate-crenulate margins and few lateral leaflet pairs (2-3) which are generally smaller than the terminals; interjected leaflets numerous; corolla white. Distribution: N. Peru, dept. Cajamarca, on mountain slopes at about 2,600 m.

37. S. coelestipetalum Vargas (Papas Sudperuanas, Cuzco, **2**, 59, 1956)

Leaf 4-jugate, with frequent interjected leaflets; lower surface densely velvety-pubescent; calyx with long, 3-4 mm., acumens; corolla bright sky-blue. (Material not seen by me.) Distribution: S. Peru; endemic to the Urubamba valley, amongst dry sparse shrubs, at 2,400 m.

38. S. colominense Cárd. (Bol. Soc. Peruana Bot., **5**, 21-23, 1956)

A small species with large terminal and rather few small lateral leaflets; corolla dark purple. A rather enigmatic species, placed by Correll as a synonym of *S. brevicaule*, and probably only a dwarf phenotype of this or some other species. Distribution: Bolivia, Cochabamba, damp mountain slopes amongst rocks, at 3,400 m.

39. S. doddsii Corr. (Wrightia, **2**, 186-87, 1961)

Leaf 3-5-jugate, glabrescent, with petiolulate laterals and very few interjecteds. Rest of green parts also ± glabrous; corolla substellate, light lavender. I have seen only a photograph of an authenticated specimen, but I am strongly of the opinion that this "species" is no more than a casual hybrid of *S. chacoense* with a blue-flowered Bolivian species or possibly an F_2 or backcross segregate from such a cross. Distribution: Bolivia, Cochabamba, on a rocky wooded slope at 3,000 m. (correct altitude?).

40.* S. huanucense Ochoa (Sol. tuber. silv. Peru, Lima, 190-92, 1962)

A striking plant with short, 1-2-jugate leaves and very large terminal leaflet; no interjecteds; laterals sessile, slightly decurrent; corolla showy, to 4 cm. diam., pentagonal to substellate, purple. Seems to have some affinities with species in Series Megistracroloba, with which it may need to be placed when it has been more fully studied.

Distribution: C. Peru, endemic to mountains of prov. Dos de Mayo, in stony rocky places, at 3,750 m.

41.* S. huarochiriense Ochoa (Sol. tuber. silv. Peru, Lima, 215-17, 1962)

Leaf with 3-4 pairs of sessile obtuse leaflets and no interjected leaflets, glabrous; corolla purple, rotate-pentagonal. (Material not seen by me.)

An interesting species of unknown affinities. Distribution : C. Peru (dept. Lima), habitat unknown, at 3,750 m.

42. S. liriunianum Cárd. et Hawkes (J. Linn. Soc., Bot., **53**, 106-08, 1945)

Leaflets narrow, with whitish pubescence ; pedicels to 3.5 cm. long ; calyx and corolla dark purple. Is possibly related to *S. vernei*. Distribution : Bolivia, dept. Cochabamba, in shady places under bushes, at 3,800 m.

43. S. lobbianum Bitt. (in Fedde, Repert., **12**, 446-47, 1913)

Stem very short ; leaf long and narrow, 3-5-jugate, with very few interjected leaflets ; stem and peduncle with long spreading hairs similar to those of *S. multidissectum* to which latter species *S. lobbianum* may be related. Distribution : S. Colombia ; exact locality not recorded, probably at ca. 3,000 m.

44. S. minutifoliolum Corr. (Wrightia, **2**, 191-92, 1961)

Leaf with two pairs of large laterals and several small ones, with about 12 pairs of minute sessile interjected leaflets ; pubescence of dense yellowish-white hairs on leaves and stems, including peduncle and pedicels ; corolla substellate. Distribution : Ecuador, in dense mountain forests on the eastern slopes of the Andes, at 1,500-2,900 m.

45. S. mochicense Ochoa (Agronomía, Lima, **26**, 111-12, 1959 ; as *S. mochiquense*)

S. carl-smithii Corr. (Wrightia, **2**, 135-37, 1961)

Leaflets 3-4(-5)-paired, sessile to petiolulate ; 3-12 pairs of interjected leaflets ; hairs quite dense but short and not easily visible ; corolla rotate, white. This curious species may be related to *S. chancayense*, or perhaps even to *S. multiinterruptum*. Distribution : N. Peru, on the lomas (low hills) by the coast, at not more than about 400 m.

46. S. mollepujroense Cárd. et Hawkes (J. Linn. Soc., Bot., **53**, 103-04, 1945)

Has affinities with *S. sparsipilum*, but differs in the long oblong leaflets and glabrescent leaf surface. Distribution : Bolivia, dept. Cochabamba, in stony bushy places.

47. S. ochoae Vargas (Papas Sudperuanas, Cuzco, **2**, 62-63, 1956)

Leaf large, 5-jugate, with numerous interjected leaflets, sparsely pubescent beneath, and with short yellowish velvety pubescence on the pedicels ; corolla rotate, dark purple. Perhaps related to *S. coelestipetalum* ? Distribution : S. Peru, amongst other herbs on a rocky mountain slope, at 3,650 m.

48. S. orophilum Corr. (Wrightia, **2**, 192-93, 1961)

Leaf with 4-5 pairs of acute to acuminate subsessile laterals and rather few interjecteds ; corolla rotate, purple. Not unlike some forms of *S. sparsipilum*. Distribution : N. Peru, on rocky bushy slopes at 3,500 m.

49.* S. paramoense Bitt. (*ex* Pittier, Man. Pl. Usual. Venez., 329, 1926)

Plant glabrescent ; leaf 3-jugate, with no interjected leaflets ; calyx glabrous ; corolla violet, up to 4.5 cm. diam., rotate. Distribution : W. Venezuela, on the páramo (high Andean grassland), at 3,300 m.

50. S. pumilum Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 124, 1944)

S. achacachense Cárd. (Bol. Soc. Peruana Bot., **5**, 30-31, 1956)

Plant with basal leaf rosette and very long peduncle (5-9 cm.); rhomboid terminal leaflet much larger than the 2-3-jugate laterals. Distribution: S. Peru, N. Bolivia; in high Andean grasslands and in stony rocky places, 3,500-4,000 m.

51.* S. regularifolium Corr. (Wrightia, **2**, 194-95, 1961)

Leaves 3-5-jugate; lateral leaflets sessile, very slightly decurrent; interjected leaflets absent; corolla substellate to pentagonal, pinkish lavender. Probably related to *S. paramoense* and possibly also to *S. colombianum* in series Conicibaccata. (Material not seen by me.) Distribution: Ecuador and N. Peru, on bushy mountain slopes at about 2,150 m.

52. S. rhomboideilanceolatum Ochoa (Rev. Argent. Agron., **19**, 234-37, 1952)

Terminal leaflet larger than the 1-3(-4)-jugate laterals; interjected leaflets few; corolla rich purple, showy, 3-4.5 cm. diam. with well-developed quadrate lobes. Distribution: C. Peru, on shrubby and grassy slopes and among rocks and cliffs at 2,900-3,500 m.

53. S. sandemanii Hawkes (Ann. Mag. Nat. Hist., Ser. 12, **7**, 709-10, 1954)

Leaf imparipinnatisect; laterals 2-3-jugate, the upper pair widely decurrent; no interjecteds; calyx lobes often sub-spathulate, very pubescent; seems to be closely related to *S. infundibuliforme* (series Cuneoalata) on the one hand, and to *S. weberbaueri* (including *S. tacnaense*) on the other. Distribution: S. Peru, dept. Arequipa, at 2,600-3,100 m.

54. S. suffrutescens Corr. (Wrightia, **2**, 183-84, 1961)

Stem stiff, rather woody; lateral leaflets sub-sessile, slightly decurrent, 4-paired with 0-2 pairs of interjecteds; calyx trilabiate; corolla purple, rotate; berries globular. Possibly related to *S. andreanum*. Distribution: Ecuador, roadside, at 2,800 m.

55. S. torrecillasense Cárd. (Bol. Soc. Peruana Bot., **5**, 15-16, 1956)

Lateral leaflets 1-3-paired, with no interjected leaflets; lower leaf surface softly pubescent; corolla rotate, blue-violet to light lavender. Allied to *S. microdontum*, but differs in the narrower leaflets and bluish corolla. Looks very similar to natural hybrids between *S. microdontum* and *S. vernei*, though I do not know whether those two species occur at Torrecillas, also. Distribution: Bolivia, dept. Santa Cruz, on rocky wooded slopes at 2,700-3,000 m.

56. S. virgultorum (Bitt.) Cárd. et Hawkes (J. Linn. Soc., Bot., **53**, 103, 1945)

S. boliviense Dun. subsp. *virgultorum* Bitt. (in Fedde, Repert., **12**, 153-54, 1913)

Rather similar to *S. microdontum* vegetatively, but with blue instead of white flowers. This species certainly needs investigation; it may perhaps represent a northern derivative of *S. microdontum*, though the corolla lobes are rather too short for that species. Distribution: N.

Bolivia, dept. La Paz, amongst bushes on high mountain slopes, at 2,700-4,050 m.

57. S. weberbaueri Bitt. (in Fedde, Repert., **11**, 365-66, 1912)

S. tacnaense Ochoa (Agronomía, Lima, **28**, 133-36, 1953)

Related to *S. medians* and *S. sandemanii*, but differs from the former in the 2-3-jugate leaf and strongly pubescent pedicel, and from *S. sandemanii* in the rather broad ovate leaflets and absence of strong decurrency. Distribution: S. Peru, amongst shrubs and rocks, and on stony hillsides, both in the coastal lomas and higher up in the mountains; from 500-3,200 m.

Cultivated species

58. S. ajanhuiri Juz. et Buk. (Proc. U.S.S.R. Congr. Genet., **3**, 605, 1929)

This species is similar in many respects to *S. stenotomum*. It differs, however, in the small regular calyx, smaller blue flower, very high pedicel articulation, and stiff leaves. Agrees with *S. stenotomum* in the decurrent bases of the uppermost leaflet pair and in the form of corolla. It was possibly derived from *S. stenotomum* by a complex series of natural crosses. Frost resistant. Distribution: N. Bolivia, dept. La Paz, at high altitudes. 2n = 24.

59. S. × chaucha Juz. et Buk. (Proc. U.S.S.R. Congr. Genet., **3**, 609, 1929)

S. coeruleiflorum Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., 131, 1944)

S. mamilliferum Juz. et Buk. (Proc. U.S.S.R. Congr. Genet., **3**, 609, 1929)

S. tenuifilamentum Juz. et Buk. (Proc. U.S.S.R. Congr. Genet., **3**, 603, 1929)

I have grouped under this name all those triploid forms that have been derived from natural crosses between *S. tuberosum* subsp. *andigena* and *S. stenotomum*.[1] Some of these, which are most distinct and more widely cultivated, were formerly classed by Juzepczuk and Bukasov (1929) and by myself (1944) as separate species. Many more collections of triploid cultivated potatoes have been made, each of which differs in certain points

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[1] Bukasov (1939) considers that *S.* x *chaucha* was derived from *S. phureja*. From morphological and genetical evidence I consider this to be very unlikely.

from the micro-species already described. This is only to be expected when we consider that triploid hybrids could have been formed many times by the crossing of different clones of the two very polymorphic species *S. stenotomum* and *S. tuberosum* ssp. *andigena*. If these hybrids are to be named at all, they should be considered merely as nothomorphic forms of one species. I have therefore retained the name *S.* × *chaucha* since it was the first to be applied to these triploid forms by Juzepczuk and Bukasov. The best way of distinguishing *S.* × *chaucha* from other cultivated species is by the corolla lobes which are in general about 3 × as broad as long when spread out flat. Distribution: Central Peru to Central Bolivia at high altitudes. 2n = 36.

60. S. × curtilobum Juz. et Buk. (Proc. U.S.S.R. Congr. Genet., **3**, 609, 1929)

Distinguished by semi-rosette habit, straight stiff leaves, very high pedicel articulation and large purple *circular* corolla 30-35 mm. diam. with very short lobes and acumens. Derived from natural crosses between *S.* × *juzepczukii* and *S. tubeosum* subsp. *andigena* (see Hawkes, 1962). Numerous variations in tuber colour and form are known. Central Peru to South Bolivia at very high altitudes. Frost resistant. 2n = 60.

61. S. × juzepczukii Buk. (Proc. U.S.S.R. Congr. Genet., **3**, 603-04, 1929)

Distinguished by the semi-rosette habit, long straight leaves, short peduncle (2-4 cm. long), pedicels with very high but indistinct articulation, and small blue corolla (to 2·5 cm. diam.) with very short lobes and small acumens.

A natural triploid hybrid between *S. acaule* and *S. stenotomum* (see Hawkes, 1962) which has almost certainly been formed more than once, with different varieties of *S. stenotomum* involved in each case. Distribution: Central Peru, southwards to South Bolivia at very high altitudes. Frost resistant. 2n = 36.

62. S. phureja Juz. et Buk. (Proc. U.S.S.R. Congr. Genet., **3**, 604-05, 1929)

S. ascasabii Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 130, 1944)

S. boyacense Juz. et Buk. (Proc. U.S.S.R. Congr. Genet., **3**, 609, 1929)
S. caniarense Juz. et Buk. (in Vavilov, Theor. Bases Pl. Breed., **3**, 17, 1937 ; *nomen nudum*)
S. cardenasii Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 129-30, 1944)
S. kesselbrenneri Juz. et Buk. (in Vavilov, Theor. Bases Plant Breed., **3**, 18, 1937 ; *nomen nudum*)
S. rybinii Juz. et Buk. (Proc. U.S.S.R. Congr. Genet., **3**, 606, 1929)

Distinguished by the sparsely pubescent leaf, which is shining in the living state, and rather irregular calyx with lanceolate lobes. Tubers yield in 3-4 months under short day conditions and possess no dormancy period. This very widespread and highly variable species was formerly separated into a number of smaller units. These have been found to hybridize without lack of vigour or fertility in the F_2 generation under experimental conditions and hence cannot be considered as distinct. The absence of tuber dormancy indicates that it has become specially adapted to regions that are free from long periods of drought or frost. Distribution : Venezuela, Colombia, Ecuador, Peru and N. Bolivia. Wet mountain slopes mostly in eastern Andes, at lower altitudes than the other cultivated species. 2n = 24.

63. S. stenotomum Juz. et Buk. (Proc. U.S.S.R. Congr. Genet., **3**, 604, 1929)

S. churuspi Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 129, 1944)
S. yabari Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 129, 1944 ; *pro parte*)

Distinguished from *S. phureja* by the more densely pubescent leaf which is not shining in the living state, tubers produced in 5-6 months or longer and with definite dormancy period. Calyx generally irregular with lanceloate lobes as in *S. phureja*. A very variable species which is possibly ancestral to all the other cultivated potatoes. These have been produced from it either by hybridisation (*S.* × *chaucha*, *S.* × *curtilobum*, *S.* × *juzepczukii*, *S. ajanhuiri*) by auto- or allopolyploidy (*S. tuberosum*) or by evolutionary divergence at the same level of ploidy (*S.*

phureja). Forms with pinkish-lilac corollas from S. Peru which were formerly placed with *S. yabari* and *S. churuspi* (the latter with very short corolla lobes) have now been united with *S. stenotomum.*

Subspecies stenotomum. Includes forms with smaller flowers and unribbed calyx base ; leaflets generally 2½ times as long as broad, or even narrower.

Subspecies goniocalyx (Juz. et Buk.) Hawkes, comb. nov.

S. goniocalyx Juz. et Buk. (Proc. U.S.S.R. Congr. Genet., **3**, 605-06, 1929)
S. yabari Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 129, 1944 ; *pro parte*)

A nothern subspecies of *S. stenotomum*, with large white or pink flowers and ribbed calyx base. Tubers with bright yellow flesh.

Distribution : Subsp. *stenotomum* : South Peru to central Bolivia, at very high altitudes. Some forms are frost-resistant.

Subsp. *goniocalyx* : Central to north Peru, at high altitudes. 2n = 24 for both subspecies.

64. S. tuberosum L. (Sp. Pl., **1**, 185, 1753)

S. chiloense (A. DC.) Berth. (Ann. Sci. Agron., Paris, **28**, 179, 1911)
S. cultum (A. DC.) Berth. (Ann. Sci. Agron., Paris, **28**, 179, 1911)
S. esculentum Neck. (Delic. Gallo-Belg., **1**, 119, 1768)
S. leptostigma Juz. (Bull. Acad. Sci. U.R.S.S., **2**, 309-10, 1937)
S. maglia Schlechtd. subsp. *meridionale* Bitt. (in Fedde, Repert., **12**, 453, 1913)
S. molinae Juz. (Bull. Acad. Sci. U.R.S.S., **2**, 308-09, 1937)
S. sabinii (A. DC.) Berth. (Ann. Sci. Agron., Paris, **28**, 179, 1911 ; *pro parte*)
S. sinense Blanco (Fl. Filip, ed. I, 137, 1837)

Distinguished from the other species of cultivated potato by the pedicel articulation placed in the middle third, short calyx lobes arranged regularly, leaves often slightly arched, leaflets always ovate to ovate-lanceolate, about twice as long as broad, never narrow lanceolate as in some forms of *S. stenotomum* and *S. phureja*. Corolla lobes about half as long as broad. Tubers with well-marked dormancy period.

Two subspecies are now recognised (Hawkes, 1956) :—

Subspecies tuberosum. Originally only from the coastal regions of South Central Chile (Island of Chiloé and adjacent mainland). Is distinguished from subsp. *andigena* by the less dissected leaves with wider leaflets, generally arched and set at wider angle to stem. Pedicel thickened above ; corolla often white or pale coloured. Tubers formed under long days or under short days in the tropics at lower altitudes only (500-2,000 m.). This subspecies was derived from subsp. *andigena* probably on two separate occasions ; first in Chile, where subsp. *andigena* was carried by Indian tribes migrating southwards from the Bolivian Andes ; secondly subsp. *andigena* was brought to Europe after the Spanish conquest where under similar climatic and daylength conditions to those of Chile the typical subspecies *tuberosum* was formed again, partly as a result of artificial selection. The evidence for this is set out at length by Salaman (1937, 1949), Hawkes (1956), and Salaman and Hawkes (1949).

Subspecies andigena (Juz. et Buk.) Hawkes (Proc. Linn. Soc. Bot., **166**, 130, 1956)

S. andigena [1] Juz. et Buk. (Proc. U.S.S.R. Congr. Genet. **3**, 609-10, 1929)

S. apurimacense Vargas (Papas Sudperuanas, **2**, 58-59, 1956)

S. subandigena Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 128, 1944)

This subspecies may be distinguished by the narrower more numerous leaflets, which are generally petiolulate, the leaves set at an acute angle to the stem and generally more dissected ; pedicel not thickened at apex ; tubers formed at high altitudes only [2] (over 2,000 m.) under short day conditions. This is

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[1] Formerly written as *S. andigenum* ; orthography revised according to Index Kewensis.

[2] They are, of course, formed under experimental conditions in Europe at low altitudes, but not in the tropics where the temperatures are very high.

undoubtedly the ancestral subspecies of *S. tuberosum*, formed either partly or wholly from *S. stenotomum* in the Andes of Peru and Bolivia.

Distribution: Subsp. *tuberosum*: Primitively on the southern coast and islands of southern Chilé (Chiloe region), now world-wide.

Subsp. *andigena*: Andes of Venezuela, Colombia, Ecuador, Peru, Bolivia, N.W. Argentina; also sparingly in Guatemala and Mexico. Escaped forms of both subspecies have been described under the names of *S. apurimacense*, *S. subandigena*, *S. molinae*, *S. leptostigma*, *S. maglia*, subsp. *meridionale*, etc. They differ only in the longer stolons and sometimes unpigmented tubers from the cultivated varieties. $2n = 48$.

APPENDIX I

Names not included in the present treatment

In the list which follows I have given names which are unsatisfactory for the following reasons :—

(i) **Nomina nuda** Names proposed without any descriptions, or with inadequate descriptions published in a vernacular language, and not in Latin as required by the international laws of botanical nomenclature. In each case I have given what I think is the equivalent correct name if I have been able to elucidate this from printed, written or verbal information.

(ii) **Nomina dubia** Names with uncertain application, *e.g.*, where, although a valid description may exist, the application of the name is uncertain and not completely verifiable through lack of type material or imprecision in the description.

(iii) Names given to artificial hybrids ; these are unnecessary and should be discontinued ; complete references are given in the bibliography on p. 173.

S. amayasensis Ochoa, *nom. nud.* (Biota, **1**, 50, 1955)

S. antipochacoense Koopmans, *nom. nud.* (1951). Name given to the artificial amphiploid hybrid of **S. stoloniferum** × **S. chacoense**. (See also *S. artificiale.*)

S. antipophureja Koopmans, *nom. nud.* (1951). Name given to the artificial amphiploid hybrid of **S. stoloniferum** × **S. phureja.**

S. aquinas Bukasov, *nom. nud.* (Züchter, **28**, 65-70, 1958). Name given to Darwin's collections of wild potato from south Chile = **S. tuberosum** subsp. **tuberosum**. (See Hawkes, 1956.)

S. aracc-papa Juzepczuk, *nomen dubium* (Bull. Acad. Sci. U.R.S.S., **2**, 306-07, 1937). The original collection on which this name was based seems to have been a hybrid population of **S. raphanifolium** × **S. sparsipilum** (or possibly even *S. raphanifolium* × *S. multidissectum*). No type specimen was designated until long after the description was published, and various specimens taken from time to time in the experimental field at Leningrad differ enormously from each other, some being indistinguishable from *S. raphanifolium* and others very close to *S. sparsipilum.* To add to the confusion, even Juzepczuk's original collection seems to have been given two different numbers (1190, 1455). I am convinced that the original collection of this species was a mixed one, and I therefore think that it would be better to class *S. aracc-papa* as a *nomen dubium* and to discontinue its use.

S. arraypitense Firbas et Ross, *nom. nud.* (Z. Pflanzenz, **45**, 284, 1961).

S. artificiale Toxopeus, *nom. nud.* (1947). An artificial amphiploid hybrid of **S. chacoense** × **S. stoloniferum** and the reciprocal cross. It is therefore equivalent to *S. antipochacoense* (q.v.).

S. baccale-albescens Zhukovsky, *nom. nud.* (J. Agric. Trop Bot. Appl., **1**, 257-80, 1954). According to Bukasov (personal communication) this name was given in error to a form of **S. phureja.**

S. bonariense Bukasov, *nom. nud.* (Bull. Appl. Bot., Leningrad, Ser. A., **19**, 83-85, 1936). This is a homonym, since the name has already been applied to a non-tuberiferous species. Bukasov later renamed this taxon validly as **S. laplaticum** Buk., placing it under the collective species *S. commersonii* (in the wider sense). I consider that this is incorrect, and in the present treatment I have placed it as a synonym of **S. chacoense** (see p. 102).

S. boreale (A. Gray) Bitt. *nomen dubium* (in Fedde, Repert., **11**, 459, 1912). This may refer to *S. jamesii*, to pale flowered forms of *S. fendleri*, or even possibly to *S. polytrichon* (see p. 124).

S. brevistylum Wittm., *nom. nud.* (see Berthault, Ann. Sci. Agron., Paris, **2**, 186, 1911). There seem to be no significant differences between this and **S. fernandezianum** Phil., according to Berthault. Even if there were a valid description, therefore, the name *S. brevistylum* would probably be a synonym.

S. candelarianum Cárd. (Bol. Soc. Peruana Bot., **5**, 12-13, 1956); non *S. candelarianum* Buk. (see p. 124). This is a homonym, since the name was used by Bukasov in 1930. I have seen no type material and cannot say what the affinities of this species might be until I can see authentic specimens or photographs. Correll (1962) is of the same opinion.

S. catamarcae Bitt., *nom. nud.* This name was proposed by Bitter on the label of a collection of Schickendantz *No. 226* in Herb. Berlin. The collection has been destroyed, even though a photograph exists. The material would seem to have been a hybrid of **S. sanctae-rosae x S. venturii,** but there is some element of doubt about it, and the name should be discontinued.

S. cayeuxii Berth., *nomen dubium* (Ann. Sci. Agron., Paris, **2**, 210, 1911). Berthault published a short description in latin, but not sufficient for us to be able to distinguish this species without additional aid. No type specimen has been discovered, and although it seems likely that the material introduced by Cayeux was a Colombian form of the cultivated species **S. phureja,** one cannot be certain of this without type material.

S. chilotanum Hawkes, *nom. nud.* (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 79, 1944). A name proposed for the cultivated Chilean forms of **S. tuberosum** subsp. **tuberosum.**

S. chocclo Buk., *nom. nud.* (in Vavilov, Theor. Bases Plant Breed., **3**, 18, 1937). Published with a very short Russian description, and no latin diagnosis. It would seem that the triploid cultivars to which this name was originally applied should be classed under **S. x chaucha.**

S. chuga Buk., *nom. nud.* (Lenin. Acad. Agric. Sci., Inst. Pl. Ind., Leningrad, 40, 1933) = **S. cuencanum** Juz. et Buk. (see below).

S. ciezae Buk., *nom. nud.* A name mentioned occasionally in the Russian plant breeding literature, but with no description. It has been applied to a collection (K. 150) made by Schick in Ecuador or Colombia, of which I have seen a specimen. It undoubtedly belongs to **S. phureja.**

S. compactum Buk., *nom. nud.* = **S. mercedense** Buk. (= **S. commersonii).**

S. cuencanum Juz. et Buk, *nom. nud.* (in Vavilov, Theor. Bases Plant Breed., **3**, 18, 1937). This name has not been validated by a latin description. The type material was triploid and might have been a natural hybrid of *S. tuberosum* subsp. *andigena* x *S. phureja*, or even possibly an autotriploid form of *S. phureja*. Since there is considerable doubt about the true nature of *S. cuencanum* it would perhaps be better to discontinue the use of this name.

S. diemii Brücher, *nom. nud.* (Züchter, **30**, 77-80, 1960). An escaped form of *S. tuberosum* in the Nahuel Huapi district of S. Argentina, which Brücher claims is a natural triploid. I have seen material from the same region which should be named **S. tuberosum** subsp. **tuberosum.**

S. dolichostigma Buk., *nom. nud.* (in Vavilov, Theor. Bases Plant Breed., **3**, 72, 1937) = **S. emmeae** (according to Zhukovsky, in a written communication). This is a synonym of **S. chacoense.**

S. demissorosum Koopmans, *nom. nud.* (1951). An amphiploid hybrid of **S. demissum x S. tuberosum,** produced artificially. 2n = 120.

S. erlansonii Buk., *nom. nud.* (Bull. Appl. Bot., Leningrad, Ser. A., **19**, 83-85, 1936). A species from Bolivia (not Ecuador, as originally stated), which is probably synonymous with **S. stenotomum,** though it might be identifiable with *S. phureja.* Based on Macmillan and Erlanson's collections 440 and 451.

S. fonckii Phil. *ex* Reiche, *nom. nud.* (Fl. Chile, **5**, 351, 1910). This is equivalent to **S. tuberosum** subsp. **tuberosum** var. **guatecarum** (Bitt.) Hawkes. (See Hawkes, 1956.)

S. gandarae Buk., *nom. nud.* Variously mentioned in the Russian plant breeding literature as *S. antipoviczii* var. *gandarae* or as *S. gandarae* = **S. stoloniferum** Schlechtd.

S. herrerae Juz., *nomen dubium* (Bull. Acad. Sci. U.R.S.S., **2**, 310-11, 1911). Bukasov (verbal communication) states that the original tubers collected by Juzepczuk grew into a number of rather distinct entities. Certainly some of these were tetraploid escaped forms of **S. tuberosum,** subsp. **andigena.** Judging from the two colectotypes designated at a much later date by Bukasov, part of the material of *S. herrerae* was quite different, however, and could perhaps be a form of **S. leptophyes.** In view of the doubt and uncertainty about this species it would perhaps be better to discontinue the use of the name *S. herrerae.*

S. juanense Wittm., *nom. nud.* The name was noted on a specimen of Kurtz *No. 9828,* which has since been destroyed, but of which a photograph exists. It might be equivalent to **S. kurtzianum** Bitt. et Wittm.

S. kaufmanii Buk., *nom. nud.* (Bull. Acad. Sci. U.R.S.S., Ser. Biol., 715, 1938). Classed by Bukasov in the same sub-group as *S. aracc-papa.* The type specimen, however, is identifiable as **S. canasense** Hawkes.

S. macmillanii Buk., *nom. nud.* (Physis, B. Aires, **18**, 43, 1939). The type specimen of this species can certainly be identified as **S. stenotomum** Juz. et Buk.

S. martinezii Buk., *nom. nud.* (Bull. Appl. Bot. Genet. Plant Breed., Suppl. 58, Plate I, 1933). This was later named *S. antipoviczii* var. *martinezii* Buk., *nom. nud.* It undoubtedly should be classed as **S. stoloniferum** Schlechtd.

S. maydiforme Buk. *ex* Rybin, *nom. nud.* (Bull. Appl. Bot., Leningrad, Ser. 2 (2), 46, 1933). A triploid cultivar which could probably be placed under **S. x chaucha.**

S. mendozinum Buk., *nom. nud.* (Bull. Appl. Bot. Plant Breed., Ser. A No. 19, 84, 1936). Was later described by Bukasov under the name of **S. macolae** Buk. (= **S. kurtzianum** Bitt. et Wittm.).

S. nicaraguense Rydb., *nomen dubium* (Bull. Torr. Bot. Cl., **51**, 171-72, 1924). This species was said to have been collected by Flint in Nicaragua, and was classified by Rydberg in series Pinnatisecta. From the sublyrate leaf with decurrent laterals and enlarged terminal, and also from the filaments which are fused into a ring below, the type specimen seems to fit very well indeed with **S. commersonii.** Since the latter species comes from South America, it would seem probable that some confusion of collections or labels has taken place. Furthermore, I have searched carefully for this species in Nicaragua, without success, and could not indeed find any habitats in that country which would be suitable for a species of this sort with semi-rosette growth form. In view of the obvious doubts about the validity of *S. nicaraguense*, I consider that it should be classed as a *nomen dubium*.

S. pamiricum Perlova, *nom. nud.* (News Acad. Sci. U.S.S.R., Ser. Biol., No. 4, 81, 1953). A diploid form of the triploid **S. maglia** produced in the Pamir mountains in the Botanic Garden plots. Almost certainly the product of natural hybridization with a diploid wild species growing in the same plots.

S. papa Val., *nomen dubium* (Misc. Fondo Quijano Otero, Bogotá, **16**, 1-6, 1809). Although this name has been validly published there seems to be no type specimen. The fruits are rather long (5-7.5 cm.), but the description does not differ in other respects from that of **S. colombianum.** Unless a type specimen is found, however, it will be better to leave this species as a doubtful name, because of the fruit length.

S. paraguariense Dun. (in DC. Prodr., **13**, I, 376, 1852) = **S. renggeri** Schlechtd. (See below.)

S. pauciflorum Buk., *nom. nud.* (Bull. Appl. Bot., Leningrad, Ser. A (10), 51-60, 1934) = **S. curtilobum** (Type specimen seen).

S. pre-commersonii Kameraz, *nom. nud.* (Soviet Plant Industr. Rec., No. 4, 13, 1940). A diploid form of **S. commersonii** Dun.

S. pseudomaglia Planchon, *nom. nud.* (Ann. Fac. Sci., Marseilles, **18**, 205-24, 1909). = **S. chacoense** Bitt.

S. reddickii Buk., *nom. nud.* (in Vavilov, Theor. Bases Plant Breed., **3**, 51, 73, 1937). Later classed as *S. antipoviczii* var. *reddickii*. = **S. stoloniferum.**

S. renggeri Schlechtd., *nomen dubium* (Hort. Hal., **1**, 5, 1841). This species received such a short description that it is quite impossible for us to know which species Schlechtendal had in mind, and it is doubtful whether he himself did more than read through the travel notes of Rengger. No type specimen has been discovered, and from our knowledge of the potatoes of Paraguay, either *S. chacoense* or *S. commersonii* subsp. *malmeanum* may have been seen by Rengger, possibly both.

S. riobambense Juz. et Buk., *nom. nud.* (in Vavilov, Theor. Bases Plant Breed., **3**, 17, 1937). A triploid cultivar from Ecuador which received a Russian description only. No type material was preserved, and we cannot tell whether it was a hybrid of *S. tuberosum* subsp. *andigena* x *S. phureja*, or a triploid clone of *S. phureja* itself.

S. rionegrinum Lechn., *nom. nud.* (Soviet Plant Industr. Rec., No. 4, 31, 1941). A diploid form of **S. commersonii** subsp. **commersonii** which has received a Russian description only.

S. ruderale Juz., *nom. nud.* (*ex* Rybin, Proc. U.S.S.R. Congr. Genet., **3**, 473, 1929). An unpublished synonym of **S. aracc-papa** Juz., according to Bukasov (verbal communication).

S. schenckii Bitt., *nomen dubium* (in Fedde, Repert., **11**, 448, 1912). The type specimen was in Berlin and has been destroyed, but Correll thinks this Mexican species might be synonymous with *S. oxycarpum* or *S. brachycarpum* (= *S. iopetalum*). Since the description mentions a white corolla and 2-(3-) jugate leaf, the material might with more justice be placed under *S. stoloniferum*. I looked for this species at the type locality in 1949, but without success. Unless isotype material can be found the use of the name *S. schenckii* should be discontinued.

S. schizostigma Bitt., *nomen dubium* (in Fedde, Repert., **11**, 449-50, 1912). The type specimen was in Berlin and has been destroyed. The corolla of this material was also white (see above, *S. schenckii*) and I think it likely that *S. schizostigma*, which was said to be almost completely glabrous, may be related to *S. cardiophyllum* or *S. hintonii*. The very bifid stigma, however, renders it distinct from those species, and it will be impossible to identify with any certainty unless an isotype specimen is discovered.

S. schreiteri Buk., *nom. nud.* (Soviet Plant Industr. Rec., No. 4, 13, 1940). Authenticated material of *S. schreiteri*, kindly supplied by Prof. Bukasov, is synonymous with **S. acaule** subsp. **acaule.**

S. tarmense Buk., *nom. nud.* (in Vavilov, Theor. Bases Plant Breed, **3**, 19, 1937) = *S. andigena* subsp. *tarmense* Buk. according to Zhukovsky (written communication) = **S. tuberosum** subsp. **andigena** (Juz. et Buk) Hawkes.

S. triferum Schlechtd., *nomen dubium* (Hort. Hal., **1**, 6, 1841). The description was very short and no type specimen exists, since it would seem that Schlechtendal took his description from Pöppig's account of his travels in Peru. Apparently this material refers to cultivated potatoes that yielded in three months in Peru. Ochoa (1955) mentions it as a very rare cultivar at 500-700 m., but gives no further details. Possibly it represents a form of *S. phureja*, but we cannot be certain as to the plants that Pöppig described, and the name should not be used in future.

S. valenzuelae Pal. (Mem. Mus., Paris, **2**, 340, 1816.) A synonym of the *nomen dubium*, **S. papa** Val. (see above).

S. venezuelicum Kameraz, *nom. nud.* (Soviet Plant Industr. Rec., No. 4, 13, 1940). Correll equates this with his newly described species *S. woodsonii*, but I am inclined to think that it is merely a form of **S. colombianum** Dun.

APPENDIX II

Table showing classification, chromosome numbers and country of origin of wild and cultivated potato species for which the chromosome number is known

Key to countries : (1) U.S.A. ; (2) Mexico ; (3) Guatemala ; (4) Costa Rica ; (5) Panamá ; (6) Venezuela ; (7) Colombia ; (8) Ecuador ; (9) Perú ; (10) Bolivia ; (11) Paraguay ; (12) Brazil ; (13) Uruguay ; (14) Argentina ; (15) Chile.

SERIES	SPECIES ARRANGED ACCORDING TO CHROMOSOME No. (x = 12)				
	2 x	3 x	4 x	5 x	6 x
I. JUGLANDIFOLIA	S. juglandifolium (4, 6, 7, 8) S. lycopersicoides (9) S. ochranthum (7, 8, 9) S. rickii (15)				
II. ETUBEROSA	S. brevidens (14, 15) S. etuberosum (15) S. fernandezianum (15)				
III. MORELLIFORMIA	S. morelliforme (2, 3)				

SERIES	SPECIES ARRANGED ACCORDING TO CHROMOSOME NO. (x = 12)				
	2 x	3 x	4 x	5 x	6 x
IV BULBOCASTANA	S. bulbocastanum (2, 3) S. clarum (3)	S. bulbocastanum (2)			
V. PINNATISECTA	S. brachistotrichum (2) S. cardiophyllum (2) S. jamesii (1, 2) S. michoacanum (2) S. pinnatisectum (2) S. sambucinum (2) (S. stenophyllidium ?) (2)	S. cardiophyllum (2)			
VI. COMMERSONIANA	S. chacoense (10, 11, 12, 13, 14) S. commersonii (11, 12, 13, 14) S. tarijense (10, 14) S. yungasense (10)	S. chacoense (14) S. commersonii (12, 13, 14)			

SERIES	SPECIES ARRANGED ACCORDING TO CHROMOSOME NO. (x = 12)				
	2 x	3 x	4 x	5 x	6 x
VII. CIRCAEIFOLIA	S. capsicibaccatum (10) S. circaeifolium (10)				
VIII. CONICIBACCATA	S. santolallae (9) S. violaceimarmoratum (10)		S. agrimonifolium (2, 3) S. colombianum (6, 7, 8) S. oxycarpum (2, 4, 5)		S. moscopanum (7)
IX. PIURANA	S. chancayense (9) S. chomatophilum (9) S. hypacrarthrum (9) S. piurae (9)		S. tuquerrense (7, 8)		
X ACAULIA			S. acaule (9, 10, 14)		S. acaule (9)
XI DEMISSA	S. verrucosum (2)			S. × edinense (2) S. × semidemissum (2)	S. demissum (2, 3) S. guerreroense (2) S. hougasii (2) S. iopetalum (2)

Series		Species Arranged according to Chromosome No. (x = 12)				
		2 x	3 x	4 x	5 x	6 x
XII	LONGIPEDICELLATA		S. × vallis-mexici (2)	S. fendleri (1, 2) S. hjertingii (2) S. papita (2) S. polytrichon (2) S. stoloniferum (2)		
XIII	POLYADENIA	S. polyadenium (2) S. lesteri (2)				
XIV	CUNEOALATA	S. infundibuliforme (10, 14, 15)				
XV	MEGISTACROLOBA	S. boliviense (10) S. megistacrolobum (9, 10, 14) S. raphanifolium (9) S. sanctae-rosae (14) S. sogarandinum (9) S. toralapanum (10)	S × bruecheri (14)			

SERIES	SPECIES ARRANGED ACCORDING TO CHROMOSOME No. (x = 12)				
	2 x	3 x	4 x	5 x	6 x
XVII TUBEROSA (wild species)	S. acroscopicum (9)				
	S. andreanum (7, 8)				
	S. × berthaultii (10)				
	S. bukasovii (9)				
	S. canasense (9)				
	S. candolleanum (10)				
	S. gandarillasii (10)				
	S. gourlayi (14)				
	S. gracilifrons (9)				
	S. kurtzianum (14)				
	S. leptophyes (9, 10)				
	S. lignicaule (9)				
	S. maglia (14, 15)	S. maglia (15)			
	S. marinasense (9)				
	S. medians (9)	S. medians (9)			
	S. microdontum (10, 14)				
	S. multidissectum (9)				
	S. oplocense (10, 14)		S. oplocense (10, 14)		
	S. pampasense (9)				

Series	Species Arranged according to Chromosome No. (x = 12)				
	2 x	3 x	4 x	5 x	6 x
XVII TUBEROSA (wild species)	S. rechei (14) S. × setulosistylum (14) S. soukupii (9) S. sparsipilum (9, 10) S. spegazzinii (14) S. venturii (14) S. vernei (14) S. vidaurrei (10) S. wittmackii (9)		S. sucrense (10)		
TUBEROSA (Cultivated species)	S. ajanhuiri (10) S. phureja (6, 7, 8, 9, 10) S. stenotomum (9, 10)	S. × chaucha (9, 10) S. × juzepczukii (9, 10, 14)	S. tuberosum (2, 3, 4, 6, 7, 8, 9, 10, 14, 15)	S. × curtilobum (9, 10)	

APPENDIX III

CITATIONS OF LOCALITIES AND TYPE SPECIMENS FOR THE NEW TAXA DESCRIBED IN THE PRESENT WORK

(1) **S. fendleri A. Gray, subspecies arizonicum Hawkes** (see p. 123)

U.S.A.: Arizona State, Cochise County, Chiricahua Mountains, Barfoot Park. Alt. 2,450-2,500 m., 29 July 1907. "Rich soil; rolling andesitic, recently pine-clad area, open westward."

J. C. Blumer 1566 (ARIZ, DS, E, F, GH, **K** (**Type**), L, NY, U, W).

Additional collections: *Blumer 1579*; *Hawkes, Hjerting and Lester 1177, 1180*; all from the same area. (Seed available.)

(2) **S. hjertingii Hawkes** (see p. 123)

MEXICO: Coahuila State, near Saltillo, Lirios, fields south of village on lower border of mountain forests. Alt. 2,300 m., 23 August 1958. "Growing as weed of cultivation."

Hawkes, Hjerting and Lester 1356 (**K** (**Type**), J.G.H.). (Seeds available.)

Additional collections: *Hawkes, Hjerting and Lester 1353, 1355, 1357, 1373, 1378, 1379*, the first three collections from Coahuila and the last three from Nuevo León State; *Hawkes 1112, 1113*; *Palmer* 305, 938 (p.p.); *C. H. Mueller 2215*; *Gregg 420*.

(3) **S. lesteri Hawkes et Hjerting** (see p. 126)

MEXICO: Oaxaca State, municipio Miahuatlán, road from Oaxaca to Puerto Angel, 16 miles south of Miahuatlán. Alt. 2,300 m., 19 October 1958. "Very damp bank above road in shade of bushes and trees; rich soil."

Hawkes, Hjerting and Lester 1714 (**K** (**Type**), J.G.H.). (Seed available.)

(4) **S. rechei Hawkes et Hjerting** (see p. 146)

ARGENTINA: prov. La Rioja, dept. Chilecito, Sierra Famatina, Guanchín Viejo, 25 January 1928. *Castellanos* (s.n.) (**BA 28/345** (**COTYPE**)).

ARGENTINA: prov. La Rioja, Sierra Famatina. *Reche* (s.n.). (Accession H. 614 as seed) (**K** (**COTYPE**), J.G.H.).

Additional material: *Reche* (s.n.). (Two collections sent as seed to Max-Planck Institut, Köln (Cologne): Accessions E.B.S. 2082, 2083).

APPENDIX IV

After the manuscript for this paper had gone to press some additional chromosome counts were kindly sent to me by Professor H. Ross, Max-Planck-Institut für Züchtungsforschung, Cologne, for certain species listed in the text without chromosome numbers and which do not therefore figure in the table in Appendix II. Some of these species had not been known previously in the living state and therefore are placed in the lists of species known in the form of herbarium material, since it was not possible to alter the format of this paper by the time these results came in. I give them below, together with series and page reference :—

S. huancabambense (Piurana) p. 115	2n = 24.
S. laxissimum (Conicibaccata) p. 110	2n = 24.
S. chiquidenum (Tuberosa) p. 141	2n = 24.
S. multiinterruptum (Tuberosa) p. 145	2n = 24.
S. sandemanii (Tuberosa) p. 153	2n = 24.
S. weberbaueri (as *S. tacnaense*) (Tuberosa) p. 154	2n = 24.

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(References to original descriptions, synonyms, etc., will be found in the section on detailed taxonomy immediately following the names of the species or subspecies concerned.)

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INDEX TO LATIN NAMES OF SERIES AND SPECIES

(Series in capitals; synonyms, homonyms, *nomina nuda* and *nomina dubia* in italics)

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