SCOTTISH PLANT BREEDING STATION
PENTLANDFIELD, ROSLIN, MIDLOTHIAN

ANNUAL REPORT

1956

CONTENTS

PAGE

STAFF 4

DIRECTOR'S REPORT—

Foreword 5
Cereals 6
Herbage Plants and Genecology 9
Potatoes 11
Root Crops 17
Sugar Beet 19

NEW VARIETIES 21

PUBLICATIONS 22

OCCASIONAL PAPERS 23

A note on clonal variation in the potato variety Majestic. G. COCKERHAM and A. W. MACARTHUR.

Potato Virus S. A. W. MACARTHUR.

A revision of the tuber-bearing Solanums. J. G. HAWKES.

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DIRECTOR'S REPORT

Foreword.—The potential value of wild species in potato breeding can readily be appreciated by reference to the part of this report that deals with current investigations. The important point is that some of these wild species contain qualities of economic value that are not present in the older commercial varieties. Constructive breeding by means of inter-specific hybridisation is relatively new but nevertheless several varieties so obtained have already been marketed in Europe and North America. While it is true that not all have proved successful there is no doubt that such a broadening of the basis of potato breeding has come to stay. In the past, species relationships have been the subject of much controversy, and since a clarification of the situation is very greatly needed we are indeed fortunate in being able to publish as an Occasional Paper a summary by J. G. Hawkes of his taxonomic studies on the tuber-bearing Solanums.

Another contribution is by A. W. Macarthur who deals with the problem of Virus S. A feature of this virus is its prevalence in potato seed stocks throughout Scotland and almost certainly elsewhere in Britain, a state of affairs that is doubtless a reflection of the difficulty of visual detection and the absence of any plant indicator. How important Virus S is to the commercial grower is not yet clear, though the limited evidence available does indicate that it is capable of adversely affecting yield. Unfortunately, there is no known source of immunity to this virus. A point of some academic interest is the probability that paracrinkle is related to Virus S. Incidentally, it is noteworthy that in the course of these investigations a virus detected by serological methods in commercial carnation varieties is thought to be latent carnation virus, which is also related to Virus S.

Aspects of the problem of variation within potato varieties is reviewed by G. Cockerham and A. W. Macarthur. In the variety Majestic they have not been able to detect any clonal variation to infection by virus X, and as far as Y and leaf-roll are concerned the position is still obscure.

It is perhaps not an exaggeration to say that root eelworm is causing potato growers most anxiety at the present time. In view of the fact that a sample population from a garden in Midlothian showed considerable adaptation to life in certain potato hybrids which were fully resistant to populations derived from farms, the possibility that different races of eelworm occur is being further examined.

In the Cereal Section the laboratory testing of oats for resistance to stem eelworm is now an integral part of the breeding routine.

As far as grass breeding is concerned, while orthodox techniques have undoubtedly been rewarding in many respects it is nevertheless true that increases in yield have been elusive, for when appropriate comparisons are made the newer strains show little if any advance upon the productive capacity of those of long standing. An attempt is, therefore, being made to see if it is possible to raise the yields of the different maturity *groups* of strains already in commercial use by applying the polycross technique modified in such a way as to obviate the need to maintain special inbred lines. Quite rightly every effort should be directed towards raising the productivity of arable grass but that is not to say that our uncultivated grasslands are unimportant, or that a detailed study of their floristic elements would not repay the effort involved. That the " problems of hill management or hill improvement can never be satisfactorily understood until fundamental information on the nature and significance of hill vegetations has been considerably amplified " is emphasised in the Hill Farm Research Committee Report. Perhaps the genecological approach will ultimately break new ground in this direction. Be this as it may, owing to the prevalence and usefulness of the natural bent-fescue types of sward, communities comprising these species have been chosen for genecological examination.

During the year " Pentland Beauty " a new potato variety field-immune from viruses X, A and B and foliage field-immune from the common strains of blight has been allocated to an Agent for multiplication and ultimate distribution, and two oat selections, Aa 733 and Aa 720, have been named " Albyn Bard " and " Albyn Empress " respectively.

Cereals.—The work of the Cereal Section during the year has been confined almost entirely to oats, and seed of both fixed and unfixed material was sown at two outside selection centres, one in Inverness-shire and one in Argyll, in addition to the Plant Breeding Station. The work carried on at all three centres was on similar lines and consisted of the recording of performance data during the growing season and after harvest. These selection centres were first established in 1953 in collaboration with the regional staffs of the North and West of Scotland Agricultural Colleges with the object of testing hybrid material at an early stage in the breeding process, and since these centres are located in markedly different environments, it was felt that types which were capable of doing well under a variety of conditions as well as those adapted to the special conditions of each environment would be revealed. Selections made at the centres continue to be grown at their respective centres until such time as they appear to be breeding true and then these " fixed lines " are multiplied at the Plant Breeding Station at Pentlandfield to provide seed for subsequent critical variety trials which are again carried out at the selection centres.

The first series of selections obtained in this way are now being multiplied at Pentlandfield, while new series of hybrids are being grown in selection beds at the three centres. Concurrent with the selection process at the centres, trials have been carried out with fixed material. One feature of particular interest in these trials has been the performance of Aa 733 in the Argyll environment. This oat appeared to us over a period of years as a possible improvement on Bell, but in trials carried out at the Plant Breeding Station and other similar environments there was little to choose between the two varieties. Table I in which the yields of the control varieties are expressed as percentages of Aa 733, shows particularly the value of testing in the environment for which the variety has been raised. It will be noted that in the West Aa 733 has been superior to other varieties in grain weight in 1953 and in both grain and sheaf weights in 1954 and 1955, whereas at the North centre it has on average been about equal to the varieties against which it was tested, and at the Plant Breeding Station it has been rather lower yielding except in the case of Bell and R 30 where it shows little difference. On the strength of the information obtained from the work at the trial centres during these three years the variety Aa 733, which has been named " Albyn Bard," will be released as an oat suitable for areas of high rainfall and low fertility in the West of Scotland.

TABLE I

GRAIN AND SHEAF WEIGHTS OF VARIETIES IN TRIALS AT SELECTION CENTRES IN 1953, 1954 AND 1955 EXPRESSED AS PER CENT OF Aa 733 (ALBYN BARD)

		Albyn Bard	Bell		R. 30		Sun II		Ayr Line		Yielder		Onward	
			Grain	Sheaf	Grain	Sheaf	Grain	Sheaf	Grain	Sheaf	Grain	Sheaf	Grain	Sheaf
P.B.S.														
High fertility	1953	100	105.8	118.0	93.7	106.7	123.7	124.8	—	—	130.0	115.0	110.4	117.5
	1954	100	100.4	119.8	95.1	104.3	140.4	124.7	111.3	106.1	112.1	107.2	113.6	106.4
	1955	100	—	—	—	—	141.7	121.5	98.7	100.3	95.3	86.1	119.8	101.8
Low fertility	1953	100	84.0	103.9	90.6	99.4	122.3	120.0	—	—	103.3	108.2	94.9	105.7
	1954	100	99.1	121.7	92.1	105.6	142.4	123.8	112.4	111.3	105.5	106.0	108.5	105.7
N. Centre														
	1953	100	—	—	88.8	88.5	112.0	105.1	—	—	—	—	107.3	92.8
	1954	100	—	—	123.3	121.7	90.0	77.2	110.0	108.9	—	—	108.3	96.7
	1955	100	—	—	93.8	95.3	87.5	82.1	90.8	91.5	—	—	104.1	96.2
W. Centre														
	1953	100	76.8	116.9	77.7	105.4	—	—	—	—	77.7	105.4	—	—
	1954	100	79.7	89.1	86.6	92.4	—	—	—	—	61.8	64.0	—	—
	1955	100	65.4	69.9	72.2	71.6	88.0	80.2	—	—	86.5	76.4	—	—

Another variety which has attracted considerable attention in the past few years when distributed for trials is Aa 720. This variety has done particularly well on heavy land where an early-ripening oat has been required. On the recommendation of the County Advisory Officers of the Agricultural Colleges, who found that this oat meets a particular need in their areas, Aa 720 has now been named "Albyn Empress." Seed of both the above varieties is already available in the districts to which they are suited and growers should contact their County Advisory Officer.

Of recent years the problem of tulip-root in oats caused by stem eelworm, *Ditylenchus dipsaci*, has been of increasing importance and a start has now been made at the Plant Breeding Station at Pentlandfield to test in the laboratory both fixed and unfixed material for sources of resistance. The technique adopted is basically that developed by Seinhorst in his work on Rye, and results to date indicate that this technique provides a convenient and rapid method of assessing the degree of susceptibility to eelworm attack.

Herbage Plants and Genecology.—The tendency both at the Plant Breeding Station and elsewhere has been to concentrate upon the separation and development of special maturity types while, at the same time, attempting to raise the yield of strains within these categories. There is, indeed, much to be said for this policy, for under modern methods of management production at a particular time may be much more important than total seasonal yield. However, it is perhaps significant that results from recent grass variety trials provide no indisputable evidence that the breeder in this country has been successful in raising yields appreciably above those attained by equivalent strains of long standing. Despite these findings, the search for yield increases continues, but it may be necessary to turn to new techniques to achieve the desired results. Accordingly, attempts are being made at the Station to utilise a modified form of the polycross method in the breeding of grass strains. This system, which is being widely applied to other crops, in its normal form consists of random crossing by natural agencies of a number of selected inbred lines derived from single mother plants, some or all of which may in themselves be the result of deliberate crossing. This type of programme involves the maintenance of large numbers of clones for the production of seed in successive years. It is thought that some of the advantages to be gained by crossing of inbred lines might be similarly obtained by employing commercially available strains from divergent environments. The Station's polycross programme is, therefore, designed to test this possibility. Such a method would have the merit of avoiding the need for maintaining large stocks of inbred material. At present two polycross trials involving seven early ryegrass strains and ten late strains of cocksfoot respectively have been laid down. In both trials each strain is represented by one hundred unselected plants.

The genecological studies now in progress have a close connection with the complex problem of hill-land improvement. The primary need at the moment is to acquire fundamental information concerning the detailed structure and potentialities of plant communities in order to gain a proper understanding of the problems involved.

It has been found that many intraspecific characters which are assumed to be of adaptive importance because of differences between populations, have in fact proved to be genetically variable within populations. This was revealed by a trial with cloned material in the experimental garden when the within-clone phenotypic or expressed variation was much less than that within populations. Under different environmental conditions, however, this genetic variability may or may not be expressed phenotypically and it is possible that a population in its own native environment would be more uniform than elsewhere. One of the difficulties in this kind of work is to recognise the environmental factor associated with any particular adaptive response. Fortunately, an example of adaptation to an overwhelming environmental factor has been detected at Leadhills in Lanarkshire. Here the character of lead tolerance in two species of grass appears as a response to a very strong selection by very poisonous soil. It is hoped to use this material to trace the spread of genes responsible for this tolerance and to relate this spread to lead contents, ages and distances apart of the various tips. The possibility of dating offers a particular attraction as we know very little about the speed with which differentiation such as this takes place in the wild. It is proposed to use the degree of root development under standard conditions as a measure of lead tolerance.

A stand of bent-fescue chosen for its comparative uniformity was found to occupy a habitat which on ecological examination was far from uniform since the surface soil pH varied from 5.0 to 6.6 in a clearly defined pattern. The possibility that population genetic variation may be coupled with such very local environmental variation in the sampling area is receiving intensive study, for which material representing five species was gathered from a 1,600 point grid over the area and is now on trial. The influence of variation in environmental factors upon the floristics of the area was, however, clear, for whereas the abundant species were more or less evenly distributed, several others were confined to, or more prevalent in, the areas of higher pH, while still others were restricted to a damp hollow on one side of the quadrat.

During the year a number of *Agrostis* population samples were taken from communities which would floristically come within the title of *Agrostis*-fescue sward. The habitats from which they were taken, however, differed considerably one from another and these differences are reflected in the plant variation. The hill *Agrostis* are represented by two taxonomic species *A. canina* and *A. tenuis* both having the same chromosome number. These two species evidently do not represent discrete units but rather the end points of a range of forms. While it has been found that some populations are virtually true *A. tenuis*, none was found to be composed solely of the *A. canina* type. The intermediates may prove to be an overlapping of the intra-group variation, or, alternatively, may comprise inter-group hybrids. The occurrence of hybrids between closely related parent species may have considerable ecological significance should they possess a degree of tolerance to environment in excess of that of either parent.

It has already been shown that the other major constituents of *Agrostis*-fescue swards, *Festuca-ovina* and *F. rubra*, are represented by different chromosome races with different inherent ecological potentialities. The occurrence of these races and the fact that they are themselves ecologically subdivided, may well stimulate a renewed interest in plant sociological methods and the possibilities of integrating the genecological and ecological findings.

Potatoes.—During the past twenty years breeding for resistance to viruses has been directed mainly towards the utilisation of resistant qualities already available in domestic varieties. Many of these qualities fall short of perfection, however, and consequently a continual search is being made for enhanced resistance among the exotic material of South America. This search has not been made in vain for highly resistant material has been discovered in many species. Only a few of the sources have been explored, however, and our own investigations have been centred upon resistance to virus Y found in *S. rybinii* and *S. stoloniferum* and immunity from virus X found in *S. acaule*.

S. rybinii is a cultivated diploid species which has long had the reputation of being resistant to virus degeneration. Recent studies have indicated that this reputation is based on two different qualities — namely, a general tendency towards tolerance of many viruses and a marked resistance to infection with virus Y. This resistance reaches a very high level in the clone C.P.C. 979 which, although not immune, is exceedingly difficult to infect. Moreover, in the few cases where infection has been detected following graft inoculation, the tuber progenies of the infected plants have invariably been free from the virus. It would seem, indeed, that the resistance operates systemically to prevent virus multiplication. Evidence confirming this view has been obtained from breeding experiments in which the resistance of C.P.C. 979 has been combined with the genes conditioning necrotic response to virus Y in *S. simplicifolium* and *S. demissum*. In their normal background, these genes are responsible for systemic necrosis leading to the death of the host plant when infected with virus Y. When transferred to the background provided by *S. rybinii*, however, the necrotic response is reduced to that of local lesion formation at the site of infection—that is, a typical hypersensitive response on the part of the host. Seedlings of the hypersensitive type as well as fully resistant seedlings have been used as parents in breeding experiments designed to transfer the resistance to commercially acceptable varieties. In this transfer, due regard has to be paid to the facts that the resistant parental material is diploid and that there is a dissipation of resistance and a weakening of hypersensitivity in the course of outbreeding. However, by the use of colchicine to double the chromosome number of *S. rybinii* hybrids and by the adoption of intercrossing and backcrossing schedules in breeding, these difficulties have been overcome and stocks suitable for commercial breeding operations are gradually being assembled.

The new systematic treatment of potato material has brought together within the species *S. stoloniferum*, the forms *S. malinchense*, *S. longipedicellatum* and *S. antipoviczii* all of which contain clones highly resistant to virus Y. Moreover, the resistant clones all behave in similar fashion towards virus Y. Thus, when inoculated with infectious sap or by infective aphids, no symptoms have been observed on the inoculated plants and no virus has been recovered from them; but when inoculated by graft infection they have responded with a necrosis which is usually localised in the growing apices, or in the young leaves of the shoots formed immediately below the graft. Susceptible clones, on the other hand, respond to all forms of inoculation with the expression of mosaic symptoms and a marked reduction in vigour. Inheritance studies have shown that the necrotic response, which, presumably, is the basis of the resistance, is dominant to susceptibility and is under the control of a single gene. The utilisation of this gene is the objective of a special breeding programme which has now advanced to the third generation in outcrossing to commercial varieties. During this passage no alteration in resistance seems to have taken place although many of the "wild" characters of *S. stoloniferum* have already been eliminated.

A high degree of resistance to virus Y has also been found in the species *S. chacoense* but as yet there is insufficient information to assess either its form or its value in breeding.

The Andean species *S. acaule* contains clones which are susceptible to virus X and express systemic mosaic disease when infected, clones which are hypersensitive to the virus and show necrotic symptoms upon infection, and clones which are immune from the virus when inoculated by either sap or graft transfers. Inheritance studies have shown that susceptibility is recessive to both hypersensitivity and immunity whilst immunity is dominant to hypersensitivity. This pattern of phenotypic relationship is similar to that found in breeding experiments involving the X-immune American seedling U.S. 41956 and domestic varieties. Genetically, however, there is a marked difference between the two forms of immunity for whereas that of U.S. 41956 appears to be controlled by two complementary genes both of which are required for the establishment of immunity, the immunity of *S. acaule* appears to be controlled by a single gene. Moreover, in *S. acaule* the gene controlling immunity appears to be an allele of the gene controlling hypersensitivity. Should these genetic differences be confirmed it would seem that in U.S. 41956 and *S. acaule* two substantially independent forms of immunity from virus X are available for use in breeding. Both forms, indeed, are already included in current breeding material.

The search for resistance to the blight fungus, *Phytopthora infestans*, that has been in progress in many different countries was responsible for the early and extensive use of the wild species *S. demissum* in interspecific hybridisation. Although the investigations on the inheritance of resistance have provided much information, the production of resistant varieties for commercial purposes has been greatly handicapped by the appearance of new specialised races of the parasite. As new resistant genotypes have been produced, new races of the fungus capable of attacking them have been found to exist in some parts of the world. Fifteen of the sixteen races we originally postulated have been distinguished, and one of them, viz. (1, 2, 3, 4), can cause disease in plants possessing all four known major genes. Several of these races were isolated from host genotypes that did not fully represent the complete host range of the isolate and may, therefore, have persisted for some time on varieties genetically different from their natural host.

In order to determine if further genes exist, tests were carried out on selfed progenies of a series of wild species indigenous to Mexico, and on hybrid derivatives of *S. demissum*, *S. salamanii* and *S. stoloniferum* obtained from reserve stocks of true seed secured a number of years ago. In the case of the selfed progenies, the reactions of the seedlings to the five races of the fungus with the widest host ranges, viz. (1, 2, 3), (1, 2, 4), (1, 3, 4), (2, 3, 4) and (1, 2, 3, 4), were examined. From the results it was possible to distinguish lines possessing new genes and to determine the actual genetic constitution of parent plants containing not more than the four genes already known, viz., R_1, R_2, R_3 and R_4. Further, in certain progenies which contracted the disease the mildness of the symptoms and the speed of recovery indicated that they contained minor genes providing a high degree of field resistance. Such field resistance is of particular value for the breeding of economic varieties since it appears to be unaffected by parasitic specialisation. The species considered to be of greater potential value in blight resistance work were *S. demissum, S. stoloniferum,* (*S. antipoviczii, S. longipedicellatum, S. malinchense, S. tlaxcalense*), *S. spectabile, S. oxycarpum,* (*S. longiconicum*), *S. bulbocastanum, S. pinnatisectum* and *S. polyadenium.*

The hybrid derivatives of both *S. demissum* and *S. salamanii* were tested with one race only, viz. (1, 2, 3, 4), for the purpose of identifying plants possessing either new major genes or a high concentration of minor genes. Many of the progenies were found to possess no such resistance and were eventually killed off by the disease. Several families, however, exhibited a wide range of reactions and the individual plants were classified into five groups according to the amount of disease in evidence. In each progeny only a small proportion of plants remained free from the disease, indicating that the effective resistance was polygenic in character and would, therefore, tend to be dissipated by further backcrossing to susceptible varieties. Accordingly, part of the breeding programme was devoted to the intercrossing of selected resistant types in order to intensify the resistance as far as possible. The most promising of this material, based on economic potentialities as well as resistance, was bred originally from *S. demissum*, but a few derivatives of *S. salamanii* were also considered worthy of further investigation. F_1 hybrids of *S. stoloniferum* resembled the wild parent in several characters, but since they exhibited valuable resistance, the breeding experiments will be continued. A few advanced seedlings also showed effective resistance and one of them has remained free from the disease during seven years of cultivation in the tropics where blight has been a serious problem.

Breeding for resistance to the potato root eelworm, *Heterodera rostochiensis*, which started in 1952, was made possible by the discovery of four clones of *S. andigenum* which remained free from cysts when grown in eelworm infested soil. Comparable resistance is not present in any commercial potato variety and is apparently very rare within the tuber bearing Solanums as a whole. Resistance is a heritable character and is manifest by the inability of the parasite to reproduce in the roots. An important feature of resistant plants is their ability to stimulate hatching of the larvæ and consequently to reduce the eelworm content of infested soils.

The improvement of the resistant clones, by means of hybridisation followed by repeated backcrossing to commercial varieties, has so far proceeded at the rate of one generation per year. This was accomplished by raising selected progenies in infested soil to determine the resistance of the individual plants, and by growing cuttings from the resistant segregates for use as parents in the field. Since the cuttings developed into strong vigorous plants they also provided data for a preliminary assessment of the relative agronomic value of the segregates. Accordingly, many of the eelworm resistant seedlings being raised in 1956 consist of third backcross progenies. Several hundred selections have been made from the preceding generations and these are being grown in trial plots to determine their possible economic value. All are immune from wart disease, many of them are field immune from virus X and some are resistant to virus Y. Resistance to blight was also incorporated in a number of the progenies.

The possible existence in nature of specialised races of the potato root eelworm or their appearance *de novo* through the selective influence of resistant plants has been kept in mind since the breeding work began. Small cysts which are occasionally found on resistant plants have been examined for their pathogenicity but in all cases they have proved to be similar to the populations from which they arose. These results are in accordance with the experience of investigators in other countries. Initial experiments to compare the pathogenicity of eelworm populations from different localities have indicated, however, that the nematode is not entirely uniform. A sample population obtained from a city garden showed considerable adaptation to life in certain hybrids which were fully resistant to other populations obtained mostly from farms. This is the first record of variation in the pathogenicity of the potato root eelworm and, although its importance is difficult to assess at this juncture, it suggests that such variation in *Heterodera* may present a problem in the future if eelworm resistant varieties become widely grown.

A first early variety bred from Craigs Royal × 1306a(2), the latter parent being derived from *S. rybinii*, *S. demissum*, Gladstone and Dr McIntosh, has been registered by the Department of Agriculture for Scotland and named " Pentland Beauty."

Root Crops.—A sample of a strain of the marrow-stem type known as "Hybrid" kale bred in New Zealand was outstanding in 1951 because its plants showed a much greater leafiness than those of marrow-stem kale which they otherwise resembled. As the season advanced and the marrow-stems became defoliated, the "Hybrid" seemed to maintain its ratio of leaf : stem by fresh growth. Its stems, however, were not very edible, and they were taller even than those of the normal marrow-stems. Since a short stem type is being sought, and as there happened to be at the Station a family of this type, M 34, it was decided to seed in isolation pairs of plants of M 34 and "Hybrid" respectively. Several F_1 progenies, M 38-M 41, were included in trials in 1953 and in October of that year, the marrow-stem kale control yielded only three-quarters as much leaf as stem, whereas the F_1 samples had twice or thrice as much. The control outyielded all the F_1 in gross weight, because its stems were twice as heavy as theirs, but in most cases the yield of leaf was in favour of the F_1. Though shorter than marrow-stem, these F_1-generation plants were definitely not short stemmed forms.

The third stage of this investigation was carried out this year with transplants in a yield trial. Eleven selected plants of the F_1 generation of M 41 had been seeded together, and F_2 progenies from six of them were tested, but inbred seed of the other F_1s was not available. There were, however, seven treatments which were offspring of various combinations of M 38, 39, 40 or 41, and these could be considered as out-crossed in comparison with the M 41 lines. The first point of interest was observed a few weeks after transplanting, when sixteen per cent of the inbred (M 41) plants were found to be dead or dying, compared with 3.6 per cent in the out-crossed F_2s and six per cent in two samples of commercial marrow-stem control. It would seem that the effects of inbreeding were manifest even though the best plants from the seed beds have been used.

Treatment		Weight in grammes		Ratio
Type	Number	Stems	Leaves	Leaf : Stem
Controls	2	1,110	980	0.9 : 1
Inbred F_2	6	450	1,290	2.9 : 1
Out-crossed F_2	7	420 to 560	1,460 to 1,670	2.6 : 1 to 4.0 : 1

The plants were spaced at two feet each way and only well grown plants with as few adjoining gaps as possible were chosen from each plot for the purpose of estimating the ratio leaf : stem, and this was done twice during the autumn and winter. The first set of figures are summarised in the table, and it will be seen that the samples of marrow-stem kale used as controls had stems twice as heavy as those of the F_2 samples, but they lacked leafage and had a ratio of leaf : stem of only 0.9 : 1. The six inbred F_2 samples were all of similar appearance, low growing and somewhat lacking in vigour, but still with three times as much leaf as stem. The out-crossed F_2, on the other hand, varied considerably in stem length and foliage characters as might be expected from their different parentage, but they were all leafy and in some cases heavy yielding.

Most of the hybrid brassicas involving thousand-headed kale × kohl rabi and/or broccoli were this year in the second generation from the forms used in the original matings, and here again considerable importance should be attached to the number of grandparents a plant possessed. In the case of a *sib* mating of parents where only two grandparents are involved the sample would be relatively inbred, whereas if two F_1 hybrids of the same combination, but of different parentage were crossed, the offspring would be relatively out-crossed. In the trial the out-crossed samples tended to be more vigorous than the inbred ; nevertheless, both forms of propagation are necessary, inbreeding to try to perpetuate favourable combinations of characters, and out-crossing to see what the combinations can perform with the aid of hybrid vigour.

A few intervarietal swede crosses are being studied and numerous " lines " which are phenotypically similar have been bred for several generations by different schedules of selfing, seeding in groups and even occasional recombinations by intercrossing within the group, with the object of obtaining a relatively uniform strain in vigorous condition. As the year 1955 produced a most abnormal swede crop notes on strain differences were worthless and applicability of yield trial data seemed questionable. However, three trials were examined, and the first which consisted of early and usually heavy cropping types had a mean root weight of 1¼ lb. and 12.5 per cent dry matter. A second trial containing hardy late types averaged 1 lb. for root weight and showed dry matter percentages ranging from 13.7 to 16.2 per cent. These were tested early in the season, but a third trial containing F_1 hybrids between pedigree lines was left till December, when it averaged 2.2 lb. root weight and 11.3 per cent dry matter. This was in the dampest area of the field. It might be added that 2.5 lb. root weight and 10-11 per cent of dry matter would be a normal expectation.

Sugar Beet.—The sugar beet research programme is mainly concerned with problems of obtaining and maintaining a strain which can withstand tendencies to bolt when sown early, or under unfavourable conditions in the northern parts of the beet growing areas. The work is undertaken at the request of the Sugar Beet Research and Education Committee of Great Britain, and is co-ordinated with that of the Plant Breeding Institute, Cambridge. Trials were sown out at Pentlandfield and also at a farm on the coast of East Lothian, which was chosen as representative of a common type of beet land. Drought in both spring and summer ruined the trials on the farm for yield purposes, but at Pentlandfield a thirteen ton per acre crop was obtained, despite much wilting of the foliage during the summer.

A trial of Cambridge material comprising KLT families was laid out at each site, and the incidence of bolting was recorded periodically. On account of the failure of the polycross samples at the coastal farm, where the objective had been yield comparison, it was decided to make yield tests on the family lines growing at Pentlandfield. Beet from a measured strip of each plot was lifted, topped and sent to Cambridge for analysis. The real purpose of the Pentlandfield trial, however, was for the selection of mother plants; these were chosen from the residual crops of eleven of the families, and also despatched to Cambridge. The object of another trial was to examine the conditions of growth suitable for steckling production, and six sowings were made in replicated plots on dates ranging from mid-March to mid-July. The numbers of surviving plants falling into a series of size grades were determined.

It had been hoped to obtain comparisons of yield of most of the Scottish raised families in the trial which failed at the coastal farm and the twenty-three samples in the Pentlandfield trial included a few of these families, but consisted mainly of progenies of plants selected for large shaws or resistance to bolting in the field. Contrary to expectation serious bolting occurred in some of these. Estimates of sugar yield and noxious nitrogen were made at the Station, and the best treatments were chosen for propagation, by means of stecklings that had been grown in seed beds concurrently with the trials. In addition to the yield trials at Pentlandfield there were large observation plots, the plants from which were lifted and carefully selected, and finally chosen on a test of specific gravity and weight. Propagation of plants selected in 1954 was carried out in isolation plots under most favourable conditions, and the Cambridge Plant Breeding Institute again kindly propagated several of the Station families. Seedlings of some Station material were subjected to continuous light for periods during the winter and early spring, with a view to separating out those genotypes which would resist bolting. There was also a considerable amount of greenhouse work done with male-sterile and monogerm sugar beet.

NEW VARIETIES

Oats

ALBYN BARD.—Suitable for areas of high rainfall and low soil fertility in western districts of Scotland.

ALBYN EMPRESS.—Suitable for heavy land where an early-ripening oat is needed.

No agents have been appointed to handle the distribution of seed of these two varieties. Elite stocks of Albyn Empress have been supplied to all three Colleges and Albyn Bard to the North and West Colleges for placing in appropriate areas. Interested growers should consult the Advisory Officers of the Agricultural Colleges who will put them in touch with local seed producers.

Potato

PENTLAND BEAUTY

Maturity.—First Early.

Tuber.—Oval (slightly flat) ; parti-coloured pink, colour in cork ; flesh pale lemon ; eyes shallow ; eyebrows long ; sprouts pink (carmine).

Foliage Type.—Home Guard.

Foliage.—Haulm of medium height, spreading with flat-topped appearance ; stems fairly numerous, green with occasional trace of colour ; nodes slightly swollen ; wings mainly straight but slightly waved at top ; leaf of medium size ; leaflets long, pointed, dark green, glossy, margins markedly waved, lobes uneven ; secondaries pointed and, like the primary leaflets, with waved margins.

Flower.—Neither buds nor flowers observed.

Remarks.—Cropping : good ; cooking quality : good ; field-immune from viruses "X," "A" and "B" ; foliage field-immune from the common strains of Blight but tubers susceptible ; moderately resistant to Dry Rot ; cracks often appear on the mature tubers if these are roughly handled.

The stock consisting of approximately 10 cwt. of tubers was multiplied in accordance with the virus tested scheme of the Department of Agriculture for Scotland. Messrs Benjamin Main & Son, Ltd., 47 York Place, Perth, have been appointed agents for the variety.

Publications

BLACK, W. (1955). Trends in potato breeding in Great Britain. *Euphytica* **4,** 223-226.

A discussion on the merits and demerits of the more widely grown varieties in this country and on the prospects of introducing resistance to viruses, wart, blight, scab and the root eelworm into new high quality varieties suitable for modern methods of cultivation and different types of soil.

BLACK W. Breeding potatoes for resistance to virus and other agents of disease. *Atti del 2° Convegno annuale della Societa Italiana di Genetica Agraria,* 1955. (In Press.)

A survey of the genetics of resistance to viruses (A, X, Y and leaf roll) blight and root eelworm in potatoes.

BLACK, W., and G. COCKERHAM (1955). Potatoes: wild plants keep this crop prolific. *Agric. Rev.* **1**(4), 20-28.

A review of potato breeding with emphasis on the value of wild species as sources of resistance to diseases and pests, particularly virus diseases, blight and potato root eelworm.

CAMERON, D. (1956). Breeding better cereals; work at the Scottish Plant Breeding Station. *Scott. Agric.* **35,** 183-186.

A review of cereal breeding at the Scottish Plant Breeding Station from its foundation in 1920 up to the present.

COCKERHAM, G. (1955). Strains of potato virus X. *Proc. second Conf. Pot. Virus Dis., Lisse-Wageningen,* 1954, pp. 89-92.

From a survey of the effects of virus X on potato varieties there emerges a pattern of relationship between strains of the virus and the two genes, Nb and Nx, which control hypersensitive response to them. Strains of the virus can be assigned to four groups; strains which activate both genes with a lethal necrotic response; strains which cause lethal necrosis in the presence of Nb but not Nx; strains which cause lethal necrosis in the presence of Nx but not Nb; and strains which activate neither Nx nor Nb and thus become systemic with non-lethal effects on varieties of all four possible phenotypes.

A NOTE ON CLONAL VARIATION IN THE POTATO VARIETY MAJESTIC

G. Cockerham and A. W. Macarthur

Evidence of clonal variation affecting yield in potatoes has been submitted by Bald and Oldaker (1950) and Davidson and Lawley (1953) and clone testing has been carried out in Holland since 1950 by the General Netherlands Inspection Service (Anon., 1950). The Dutch tests have shown that within varieties and in the absence of gross abnormalities the productive capacity of certain clones is higher than that of others. No details of standardised clone tests in this country are yet available but a number of comparisons of clonal lines of the variety Majestic have been made at various centres since 1952. By the courtesy of Mrs N. McDermott and Dr J. D. Ivins, Agricultural Experimental Unit, University of Nottingham, Mr R. Bain, North of Scotland College of Agriculture, and Dr J. L. Hardie, Department of Agriculture for Scotland, data from trials at Sutton Bonington in 1952 and 1953, at Aberdeen in 1954 and at Corstorphine in 1954 have been made available for examination. These data are given in Table I together with the results of a trial carried out at Pentlandfield in 1955.

TABLE I

Majestic clone trials. Yields in tons per acre

	Year	1952	1953	1954	1954	1955
	Location	Sutton Bonington	Sutton Bonington	Aberdeen	Corstorphine	Pentlandfield
	Form	Random Block	Random Block	Random Block	Latin Square	Latin Square
	Replicates	6	6	4	5	8
	Tubers per plot	120	120	72	80	24
Clone	46/53	9.92	18.98	16.33	15.37	16.06
	46/67	10.50	19.73	16.50	15.53	16.64
	46/78	10.93	19.65	16.88	15.83	16.94
	46/104	—	—	16.43	15.88	16.42
	4A/48	—	—	16.60	15.72	16.54
	4B/48	—	—	—	—	16.50
	D/S	—	—	—	—	16.44
	E/C	—	—	—	—	17.64
	Mean	10.45	19.46	16.55	15.67	16·65
	S.E.	0.30	0.33	0.64	0.19	0.47

Although the yields given in Table I varied greatly between centres and between years, the differences between clones in the individual trials are in no case statistically significant. A feature of interest, however, is found in comparing the five sets of data, for it is evident that clone 46/53 was consistently the poorest cropper on trial. An analysis of variance upon the yields of clones 46/53, 46/67 and 46/78 over the series shows that differences between them are highly significant as indicated below.

Analysis of variance of yield (3 clones in 5 trials)

	d.f.	S. sq.	Mean sq.	Variance ratio
Between trials . .	4	129.41	32.35	1180.76**
Between clones . .	2	1.30	0.65	23.76**
Error . . .	8	0.22	0.03	—
TOTAL	14	130.93		

** Significant at the 1 per cent level.

A comparison of the mean yields of the three clones shows that 46/67 and 46/78 outyielded clone 46/53 by 0.47 and 0.72 tons per acre, differences which are significant at the 5 per cent and 1 per cent levels, respectively.

A similar comparison between the five clones which appear in the 1954 and 1955 trials shows significant differences in yield between clones 46/53 and 46/78 and also between clones 46/53 and 4A/48. It would appear, therefore, that clonal variation within the variety Majestic may affect yield to a small but nevertheless significant extent.

Bald and Oldaker, *loc. cit.*, have pointed out that clones differ in their reactions to the varied conditions of season, soil and climate and consequently that the relationships between their yields may not be constant. In the present case, however, clone 46/53 showed consistently lower productivity over the whole series of trials. This consistency suggests that its low yielding capacity is an inherent characteristic of the clone. Conversely, the relatively high yields of clone 46/78 over the whole series of trials suggests that this clone is inherently capable of producing a slightly higher yield than most clones under varied conditions. The particularly high yield of clone E/C in 1955 is of interest. In this single trial it produced the equivalent of at least 1 ton to the acre more than the majority of clones with which it was compared and it will be of interest to see if this performance is repeated in subsequent trials.

The yield trial at Pentlandfield was carried out in association with other trials laid down in 1954 to investigate the possibility of clonal variation affecting field resistance to the X, Y and leaf roll viruses. Each trial contained 100 tubers of the 8 clones arranged in 50 plots with appropriate infector sources planted in rows between the 2-tuber units forming the plots.

Infection was evaluated in 1955 on plants grown from two tubers taken from each of the 800 plants in the trial in 1954. All three viruses were found to be uniformly distributed over their respective trial areas but whereas virus X had spread to 53 per cent of the material under test only 3 per cent of plants were infected with virus Y and 6.6 per cent with leaf roll. Details of the distribution of infection amongst the clones are given below.

TABLE II

Clone	Number of Plants per 100 infected with		
	Virus X	Virus Y	Leaf roll
46/53	57	3	6
46/67	58	9	7
46/78	60	6	9
46/104	56	3	3
4A/48	54	0	5
4B/48	49	0	6
D/S	41	2	10
E/C	49	1	7
Mean	53	3	6.6

Interclonal differences in susceptibility to virus X are not significant and, indeed, they are too small to have any marked effect on the rate of stock degeneration through virus infiltration. Differences in susceptibility to virus Y, on the other hand, are significant at the 1 per cent level and those for leaf roll fall just short of significance. The total infections with both virus Y and leaf roll were small, however, and the data may, therefore, be misleading. They are of sufficient interest nevertheless to justify further trial.

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POTATO VIRUS S

A. W. Macarthur

Potato virus S was first recorded in the Netherlands when it was detected at the Laboratory for Flower-Bulb Research at Lisse in 1948 by pathologists attempting to produce an antiserum to potato virus A. An antiserum was obtained which reacted positively with sap from potato plants which were known to be free from virus A and further work demonstrated the presence of a virus which was found to be readily sap transmissible.

Virus S has been found in many potato varieties in the Netherlands and has also been recorded in France and Germany. The finding of virus S in potato stocks in Scotland was an indirect result of the serological detection of a latent carnation virus by Kassanis. In 1953, using latent carnation virus antiserum, he obtained positive reactions with sap of several potato varieties supplied by this Station. These reactions suggested the presence of a latent potato virus, the existence of which had been suspected when many potato plants showing a transient chlorosis in the field failed to give positive results in the tests for all known potato viruses.

Arran Victory plants of healthy appearance that had reacted positively with Kassanis's antiserum were used to prepare an antiserum and, by courtesy of Mr J. M. Todd of the Department of Agriculture for Scotland, a small quantity of van Slogteren's virus S antiserum was obtained. Tests on a number of potato varieties with these two antisera and with a carnation latent virus antiserum kindly provided by Dr Kassanis were in agreement. This established a relationship between latent carnation virus and the virus in Scottish potato stocks. The virus detected in our potato varieties was thought to be very similar to if not identical with potato virus S of the Netherlands.

Observations on Infected Plants

Careful observations on plants known from serum tests to be healthy and infected respectively, have revealed that a number of potato varieties show slight abnormalities when infected with potato virus S. In many varieties, an infected plant is often lighter in colour and may show some chlorosis, particularly at the apex, which usually becomes less obvious as the plant ages (Figs. 1, 2 and 3). Reports from Holland have ascribed an obvious mosaic in certain varieties to infection with potato virus S, but such obvious symptoms have not been seen in this country. The leaflets of infected plants are frequently less fleshy, presenting a somewhat "papery" appearance and the terminal leaflets in particular show a greater tendency to drooping (Fig. 3). The surface of the leaflets is often slightly rugose and the veins may have a sunken appearance. As the plant ages, the stems may collapse prematurely outwards from the base and this, together with the drooping of the leaflets, presents a more open habit than that of a healthy plant.

THE HOST RANGE OF POTATO VIRUS S

Attempts to find hosts and possible specific indicators in a range of material excluding potato has not met with success. The following species have all failed to give a positive reaction with S antiserum following sap inoculation from S-infected Arran Victory :—

> *Nicotiana tabacum* cv. White Burley, *N. glutinosa*, *Lycopersicon esculentum* cv. Essex Wonder, *Datura stramonium*, *Gomphrena globosa*, *Solanum nodiflorum*, *Lycium rhombifolium*, *Nicandra physaloides*.

YARWOOD and GOLD (1955) claimed that cotyledons of guar, *Cyamopsis tetragonoloba*, developed small local lesions following sap inoculation with virus S. Cotyledons of guar seedlings raised from seed kindly supplied by Dr C. E. Yarwood were inoculated during March-April with several sources of virus S and also potato viruses X, A and Y, but no lesions were observed. The inoculations were carried out at two mean greenhouse temperatures, 65° F. and 70° F.

SEROLOGICAL METHODS

Serological methods offered the only certain means of detecting virus S. Methods of serum production which have been adopted are simpler than those described by VAN SLOGTEREN and the antisera have proved to be quite adequate for the routine detection of virus S. Any titre to normal plant constituents, if detectable at all, has always been negligible

FIG. 1.—POTATO VARIETY ARRAN PILOT: HEALTHY PLANTS (right) AND S-INFECTED PLANTS.

FIG. 2.—APEX OF HEALTHY PLANT OF ARRAN PILOT.

FIG. 3.—APEX OF S-INFECTED PLANT OF ARRAN PILOT.

compared with the titre to virus S. Symptomless Arran Victory plants have been used as the standard source of antigen. Usually titres of up to 1,000 were obtained. One antiserum proved to have a titre of 32,000 but the cause of this exceptionally high value is not known. Slide agglutination tests on plants which were sampled at not too early a stage of growth gave consistent results. Greenhouse material grown in the winter months did not always behave consistently when tested by slide agglutination. It was found that agglutination tests on the variety King Edward sometimes failed to give clear cut results even when well grown plants from the field were tested.

For work of a more critical nature the tube precipitation test was used. Using this method, a tuber of S-infected Arran Victory that had been treated with rindite and sprouted in the light at laboratory temperature was examined serologically during the winter period. The results are given in Table I.

TABLE I

TITRATION OF VIRUS S IN TUBER OF A. VICTORY

	Sprouts	Cortex	Outer Medulla	Inner Medulla
TITRE	256	32	16	4

Virus S was also detected in unsprouted tubers of Duke of York and it is suggested that serological examination of potato tubers would provide a useful method for selecting healthy stocks at a time when foliage may not be available for testing. The following method was found to be the most satisfactory for preparing tuber material for test by the precipitation method :—Sprouts of about one inch in length which had been hardened off in daylight were ground in a mortar, one or two drops of a 0.2 per cent solution of potassium cyanide being added during grinding. Sap was expressed through muslin, diluted to 1/8 to 1/16 with physiological saline and centrifuged for about ten minutes at 3,000 g. Extracts of other tuber tissues were used at a lower dilution.

THE DISTRIBUTION OF VIRUS S

The virus was found to be widespread and in several of the older commercial potato varieties no healthy plant was detected even after the examination of stocks from different districts of Scotland.

The virus has been detected in plants of the following varieties :—

AQUILA, ARRAN BANNER, ARRAN PEAK, ARRAN PILOT, CATRIONA, CRAIGS ALLIANCE, DOON STAR, DR MCINTOSH, DUKE OF YORK, ECLIPSE, EDGECOTE PURPLE, GLADSTONE, GOLDEN WONDER, HARBINGER, HOME GUARD, KATAHDIN, KERR'S PINK, KING EDWARD, MAJESTIC, NINETYFOLD, ORION (British), PANTHER, PARNASSIA, PENTLAND ACE, PRESIDENT, REDSKIN, UP-TO-DATE.

No natural infections have been found in the following varieties :—

ARRAN PEAK, CRAIGS DEFIANCE, CRAIGS ROYAL, DUNBAR ROVER, DUNBAR STANDARD.

In this survey no S-free plant of the following British varieties has been found :—

ARRAN VICTORY, BRITISH QUEEN, DUKE OF YORK, ECLIPSE, EPICURE, KING EDWARD.

Tests on foliage of several American potato varieties which had been obtained from Dr R. H. Larson in the winter of 1953-54 and raised in isolation under glass early in 1954 gave positive results and suggested that virus S was present in the U.S.A. All plants tested of the following varieties reacted positively :—

EARLY GEM, LA SALLE, PONTIAC, RUSSET BURBANK, SEBAGO, TRIUMPH, WARBA, WHITE CLOUD.

This was confirmed later in the same year by tests made in the Netherlands on a duplicate range of varieties from the same source. Virus S has also been found in all plants of U.S.D.A. seedling 41956 and of the variety Katahdin which were tested at this Station.

Foliage of several commercial varieties of carnation, provided by Mr S. F. Hayes, Edinburgh School of Agriculture, was examined and two varieties, ALLWOOD'S MARKET PINK and SPECTRUM SUPREME, reacted positively with S antiserum ; it was concluded that they were infected with latent carnation virus. Attempts to infect potato, tomato, tobacco and *Datura* with this virus were all unsuccessful. Infected sap from Allwood's Market Pink was inoculated to guar cotyledons in the greenhouse but no lesions were observed to develop.

Resistance and Immunity

The examination of both commercial and wild potato material has so far indicated the presence of neither immunity nor hypersensitivity to the Arran Victory source of virus S. However, some commercial varieties, in particular Craigs Defiance, appear to have some degree of resistance to infection by sap inoculation under greenhouse conditions. All plants of the following clones of wild species which had been sap inoculated from symptomless Arran Victory reacted positively with S antiserum and repeated inoculations were not found to be necessary to establish infection :—

C.P.C. No.	
1.2	*Solanum demissum*
1.3	,, ,,
3.1	,, ,,
4.5	,, ,,
4.6	,, ,,
7.3	,, ,,
7.5	,, ,,
8.4	,, ,,
14.2	,, ,,
19.1.1	,, ,,
19.1.2	,, ,,
20.1	,, ,,
21.5	,, ,,
27.3	,, ,,
43.2	,, ,,
43.3	,, ,,
44a2	,, ,,
44b2	,, ,,
47	,, ,,
47.3	,, ,,
1342.2	,, ,,
1344.2	,, ,,
1345.1	,, ,,
1346.1	,, ,,
1352.4	*Solanum demissum*
1364.3	,, ,,
2095.2	,, ,,
2097.1	,, ,,
2098.1	,, ,,
2098.3	,, ,,
2102.1	,, ,,
2102.2	,, ,,
2103.1	,, ,,
2168	,, ,,
2318	,, ,,
2336	,, ,,
12.1	*S. malinchense*
528.7	*S. acaule*
71	*S. brevimucronatum*
979	*S. rybinii*
1074	*S. andigenum*
1157	*S. chacoense*
28.2	*S. stoloniferum*
133.2	,,
2092	,,
2094	,,
2301	*S. pinnatisectum*

The Significance of Virus S to the Potato Grower

From the available evidence, it would appear that virus S is of importance to the raiser of virus-tested potato stocks and to the general potato grower. According to Brust (1955), losses in yield due to infection by the virus may be as high as 20 per cent and MUNSTER and PELET (1954) have reported yield reductions of 12.7 per cent ± 1.07 per cent in the variety Bintje. Preliminary yield trials carried out at this Station in 1955 with the varieties Craigs Alliance and Kerr's Pink tended to confirm these results. On the other hand, trials in France with a potato seedling showed no significant differences between the yields of healthy and S-infected plants. Infected plants tend to produce a large proportion of small tubers and it is evident that the selection of seed-size tubers for propagation may result in a higher number of infected plants in the crop that follows.

The transmission of virus S in the field by foliage contact and by cultivating operations may prove to be as frequent as it is in the case of virus X. An experiment carried out under glass with virus-tested plants of Arran Peak resulted in successful transmission by deliberate handling of foliage. The results of field transmission trials carried out in 1955 are not yet available.

The greatest difficulty for the seed grower, without adequate facilities for serological testing, is that of recognising an infected plant by observation. The best solution, until such time as the plant breeder may assist by the production of immune potato varieties, is that of clonal selection coupled with intensive serological testing in close co-operation with an appropriate institute. Meanwhile, hygiene applicable to the control of virus X should prove to be equally effective against the spread of virus S. No aphid vector is known for virus S.

PARACRINKLE AND POTATO VIRUS S

The existence of a virus latent in many potato varieties and the presence of paracrinkle virus in all plants of the variety King Edward suggests that the two viruses might be related.

The following arguments may be developed to support this theory :—

1. Virus S antiserum reacts with sap from all King Edward plants, demonstrating the presence in King Edward of a virus related to virus S. The reaction is, however, weaker than the homologous reaction, suggesting that the two viruses are not identical. The individuality of these viruses was demonstrated by absorbing virus S

antiserum with King Edward sap when, after the absorption, the serum still reacted with sap containing virus S.

2. Although paracrinkle virus is said to be found naturally only in plants of the variety King Edward and virus S has been found in a large number of varieties, the apparent limited distribution of paracrinkle virus may be due in part to cross-protection afforded by the widespread occurrence of virus S.
3. It is widely believed that paracrinkle has no natural means of spread. However, it has been shown by BAWDEN, KASSANIS and NIXON (1950) that it is possible to transmit paracrinkle virus by sap inoculation and it is possible, therefore, that paracrinkle may be transmitted to a limited extent by contact in the field. The fact that no such transmission has been recorded may be due in part to the difficulty of distinguishing infected plants of some varieties.
4. Bawden *et al.* recorded rod-shaped particles in King Edward sap and similar particles in paracrinkle-infected and paracrinkle-free Arran Victory sap. Rod-shaped particles of the same dimensions and form have been seen also in sap from plants known to be infected with virus S (DE BRUYN OUBOTER, 1951; GOLD, HERBERT and OSWALD, 1955; WETTER and BRANDES, 1955).

Two experiments were carried out to test the hypothesis that the reactions ascribed to paracrinkle virus and the serological reaction between King Edward sap and potato virus S antiserum were attributable to the same virus. In both experiments attempts were made to dissociate the serological reaction from known infection with paracrinkle.

In the first experiment 6 plants of each of the varieties Craigs Defiance, Craigs Snow-white and Arran Banner were grafted with scions from King Edward to establish the response to infection. A further 6 plants of each variety and also Tomato and *Datura* plants were inoculated with King Edward sap.

The presence of paracrinkle virus was detected by observation and grafting to Arran Victory plants in which the virus causes a characteristic mottle. Tests were made for virus S by serological methods with an antiserum prepared from paracrinkle-free Arran Victory plants. As a precaution, plants showing symptoms were tested for other potato viruses. The varieties Craigs Defiance and Craigs Snow-White are hypersensitive to viruses X, A, B and C and were tested for virus Y only, on leaves of an appropriate hypersensitive *Solanum demissum*. The results are given in Table II.

TABLE II

Plant No.	Arran Banner		Craigs Defiance		Craigs Snow-White		Tomato	*Datura*
	graft	inoc.	graft	inoc.	graft	inoc.	inoc.	inoc.
1	PS	H –	PS	PS	PS	PS	PS	H –
2	PS	PS	PS	H –	PS	PS	PS	H –
3	PS	H –	PS	H –	PS	H –	PS	H –
4	PS	H –	PS	H –	PS	PS	PS	H –
5	PS	PS	PS	H –	PS	PS	PS	H –
6	PS	H –	PS	H –	PS	PS	PS	H –

P = paracrinkle demonstrated.
S = positive reaction with S antiserum.
H = absence of paracrinkle.
– = negative serological reaction.

The response to infection with paracrinkle virus was found to vary with variety. Craigs Defiance plants developed a severe mottle similar to that of a paracrinkle-infected Arran Victory, Arran Banner plants an obvious chlorotic veinal mottle, while plants of Craigs Snow-White showed no symptoms.

All plants reacting with virus S antiserum induced symptoms of paracrinkle when grafted to Arran Victory plants.

In the second experiment, 4 tubers of King Edward were heated in a small enclosed box placed on a hot water radiator for five days. A thermometer sunk into one of the tubers recorded 42° C. at the end of the period of heating. The sprouts which were about 1/8 in. in length were dissected from the tubers and cultured under glass but only one survived to produce a plant. This plant reacted positively to S antiserum and when grafted to Arran Victory induced symptoms of paracrinkle. The heat treatment had failed to separate paracrinkle and a virus reacting with S antiserum.

Thus in no plant in either of the two experiments was the response of paracrinkle dissociated from a positive reaction with S antiserum. It is possible that in every case where infection was established by sap inoculation, two viruses had been transmitted together—one paracrinkle and the other a strain of virus S. The failure to separate two distinct viruses from King Edward, however, is regarded as being of some significance and it is tentatively concluded that potato virus S is serologically related to paracrinkle virus.

The relationship between paracrinkle virus and the potato variety King Edward has been used in support of certain theories of the origin of viruses (DARLINGTON, 1944, 1949; VAN DER PLANK, 1948). If the paracrinkle virus is a strain of virus S and is related to latent carnation virus, then the relationship between King Edward and paracrinkle is not unique and cannot be used to support such theories.

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A REVISION OF THE TUBER-BEARING SOLANUMS

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ERRATUM

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Page references have been printed in error and should read one more than printed—*i.e.*, 40 should be 41.

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identification. By this means it is hoped that the potato breeder will be able to verify the identity of the material on which he is working and to view his material in relation to the totality of potato species now known.

I have also tried to present a classification more in accord with modern cytogenetical views of potato species and have been able thereby to reduce the number of recognized species by nearly half. In addition to the keys, short descriptions of the species now recognized have been included, together with their synonyms and references to the sources of the original descriptions in accordance with modern taxonomic requirements. In a paper of this length there is unfortunately not space enough to discuss the detailed taxonomy, phylogeny, cytology or breeding behaviour of each species, but this is being prepared in detail for publication later in book form; nor has it been possible to give details of the classification of sub-species or varieties, together with their botanical literature citations, though sub-species have been mentioned in some cases where it was thought to be necessary for the clarification of nomenclatural points.

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A REVISION OF THE TUBER-BEARING SOLANUMS

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The very large number of species of wild and cultivated potatoes described in the literature of many countries, often in relatively obscure journals, has made the publication of a complete account of this group long overdue. Another difficulty that has been very evident is the lack of artificial keys for the identification of potato species, though this was in part met by Correll's excellent work on the Mexican and Central American species, published in 1952. Until now, however, the South American potatoes have not received monographic treatment and no complete keys for their identification have been published.

In the present work I have attempted to fill this gap by giving a conspectus or general outline of all the tuber-bearing *Solanum* species, together with dichotomous keys for their identification. By this means it is hoped that the potato breeder will be able to verify the identity of the material on which he is working and to view his material in relation to the totality of potato species now known.

I have also tried to present a classification more in accord with modern cytogenetical views of potato species and have been able thereby to reduce the number of recognized species by nearly half. In addition to the keys, short descriptions of the species now recognized have been included, together with their synonyms and references to the sources of the original descriptions in accordance with modern taxonomic requirements. In a paper of this length there is unfortunately not space enough to discuss the detailed taxonomy, phylogeny, cytology or breeding behaviour of each species, but this is being prepared in detail for publication later in book form; nor has it been possible to give details of the classification of sub-species or varieties, together with their botanical literature citations, though sub-species have been mentioned in some cases where it was thought to be necessary for the clarification of nomenclatural points.

In the main then, this paper is a summary of the revised classification of potato species which will eventually appear in less condensed form, and as such 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 sub-specific or varietal rank, and his species were generally based on only one or at the most a very few specimens. The Russian botanists and plant breeders, notably Juzepczuk and Bukasov, followed Bitter's methods fairly closely though mostly on the basis of 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, sub-species or variety. Their most important contribution to this field was undoubtedly the discovery of a number of species within the cultivated potatoes of South America, occurring in a polyploid series (Rybin, 1930 ; Bukasov, 1933, etc.)—a fact that certainly had not been guessed at before this time.

The present writer, working during the war on the collections of potatoes brought back by the Empire Potato Collecting Expeditions 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 sub-section *Hyperbasarthrum*, and to this end 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 became quite clear that the species must be regarded as larger units, comprising a rather wide range of infraspecific variability which could not be "tied down" in many cases to the Linnean varieties and forms.

Before attempting to publish a revision of this group based on herbarium studies only it was considered of vital importance to check these conclusions by experimentation. Hybridization experiments 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 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 rôle 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 in many regions 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, screes and 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, on the one hand, 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; and on the other hand, a particularly successful genotype will be able to exist almost indefinitely (depending on the conditions noted above) by means of clonal propagation. 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 all highly sterile. 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. 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.

These 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*, *S. polyadenium* 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 height between 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* is the frequent occurrence of natural hybridization in the areas where two species overlap in their geographical or altitudinal ranges. In view of the almost complete absence of sterility barriers (some species being kept apart largely by means of geographical or altitudinal barriers) and the absence also of complete genome differentiation in the sub-section, this natural hybridization is not surprising. Nevertheless, in spite of hybridization the species maintain themselves probably in most cases as distinct entities. There is some evidence, however, that introgression is taking place in certain regions, notably N.W. Argentina and the Peru-Bolivian highlands.

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, is of special 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 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 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 sub-sections. Of these, only the first, *Tuberarium*, need concern us here, since it contains the potatoes and related species. They are distinguished by a jointed or articulated pedicel and generally imparipinnate leaves.

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 sub-sections (including *Tuberarium*) then being regarded as sections. He also divided *Tuberarium* into two sub-sections, namely :—

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

Sub-section *Hyperbasarthrum* was further subdivided into groups or series by various authors. In the present work seventeen of these series are recognized, 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 Sub-section 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 given in order of ascending chromosome number, and alphabetically at each level of ploidy.

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

(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. 101.

In addition I have included for easy reference a table (pp. 43-47) 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.

Table showing Classification, Chromosome Numbers and Country of Origin of Wild and Cultivated Potato Species that have been Studied in the Living State *

Key to countries: (1) U.S.A.; (2) Mexico; (3) Guatemala; (4) Costa Rica; (5) Panama; (6) Venezuela; (7) Colombia; (8) Ecuador; (9) Peru; (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)				
II ETUBEROSA	S. brevidens (14, 15) S. etuberosum (15) S. fernandezianum (15)				
III MORELLIFORMIA	S. morelliforme (2, 3)				
IV BULBOCASTANA	S. bulbocastanum (2, 3)	S. bulbocastanum (2)			

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Series	Species Arranged according to Chromosome No. (x = 12)				
	2 x	3 x	4 x	5 x	6 x
V CARDIOPHYLLA	S. cardiophyllum (2) S. ehrenbergii (2) S. sambucinum (2)	S. cardiophyllum (2) S. ehrenbergii (2)			
VI PINNATISECTA	S. jamesii (1, 2) S. pinnatisectum (2)				
VII COMMERSONIANA	S. chacoense (11, 12, 13, 14) S. commersonii (12, 13, 14) S. tarijense (10, 14) S. yungasense (10)	S. chacoense (14) S. commersonii (13, 14)			
VIII CIRCAEIFOLIA	S capsicibaccatum (10)				
IX CONICIBACCATA	S. santolallae (9) S. violaceimarmoratum (10)		S. colombianum (6, 7, 8) S. oxycarpum (2, 4, 5)		S. moscopanum (7)

Series	Species Arranged according to Chromosome No. (x = 12)				
	2 x	3 x	4 x	5 x	6 x
X **PIURANA**			S. tuquerrense (7, 8)		
XI **ACAULIA**			S. acaule (9, 10, 14)		
XII **DEMISSA**	S. verrucosum (2)			S × edinense (2) S × semidemissum (2)	S. brachycarpum (2) S. demissum (2, 3) S. guerreroense (2) S. spectabile (2)
XIII **LONGIPEDICELLATA**		S. × vallis-mexici (2)	S. fendleri (1, 2) S. polytrichon (2) S. stoloniferum (2)		
XIV **POLYADENIA**	S. polyadenium (2)				

Series	Species Arranged according to Chromosome No. (x = 12)				
	2 x	3 x	4 x	5 x	6 x
XV CUNEOALATA	S. infundibuliforme (10, 14, 15)				
XVI MEGISTACROLOBA	S. megistacrolobum (9, 10, 14) S. raphanifolium (9) S. sanctae-rosae (14) S. toralapanum (10)				
XVII TUBEROSA (Wild Species)	S. andreanum (7, 8) S. berthaultii (10) S. boliviense (10) S. canasense (9) S. gourlayi[1] (14) S. gracilifrons (9) S. kurtzianum (14) S. leptophyes (9, 10, 14) S. maglia (14) S. marinasense (9) S. medians (9)	S. maglia (15) S. medians (9)			

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[1] Chromosome number not definitely known.

Series	Species Arranged according to Chromosome No. (x = 12)				
	2 x	3 x	4 x	5 x	6 x
XVII TUBEROSA (wild species)	S. multidissectum (9) S. neohawkesii (9) S. oplocense (10, 14) S. pampasense (9) S. × setulosistylum (14) S. simplicifolium (10, 14) S. soukupii (9) S. sparsipilum (9, 10) S. vernei (14) S. wittmackii (9)		S. sucrense (10) S. wittmackii[1] (9)		
TUBEROSA (Cultivated Species)	S. ajanhuiri (10) S. goniocalyx (9) 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)	

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[1] According to Bukasov (1938, 1941), *S. wittmackii* is tetraploid. Possibly autotetraploid races of this species are to be found, though this phenomenon has not been noted for any other wild potato species.

KEY TO SERIES WITHIN SUB-SECTION HYPERBASARTHRUM

1. Flowers bright yellow; stem woody; no stolons or tubers . . . . . **I Juglandifolia** (p. 50)
   Flowers white, cream, purple, pink, etc.; stem ± herbaceous 2
2. Pedicel articulation situated at or very near base (0-4 mm.); no stolons or tubers; berries round **II Etuberosa** (p. 51)
   Plant without the above combination of characters . 3
3. Corolla stellate, its lobes 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 12
4. Berries long conical or ovato-conical, more than 1½ times as long as broad 5
   Berries round or very slightly oval, less than 1½ times as long as broad 7
5. Plant with very wide often subcordate terminal leaflets; laterals greatly reduced or absent; flower white, less than 1.5 cm. in diameter . **VIII Circaeifolia** (p. 62)
   Plants with well-developed lateral leaflets, or if these are small, then corolla at least 2.5 cm. in diameter . 6
6. Plants with acuminate leaflets **IX Conicibaccata** (in part) (p. 63)
   Plant with obtuse or rounded leaflets **VII Commersoniana** (in part) (p. 58)
7. Flowers very small, not more than 1.5 cm. diam.; anthers narrow, somewhat adhering to each other laterally; plant generally epiphytic **III Morelliformia** (p. 53)
   Flowers more than 1.5 cm. diam.; anthers ± ovate-lanceolate, free; plants terrestrial 8
8. Corolla lobes narrow, more than twice as long as broad, or if shorter deep cream in colour 9
   Corolla lobes broad, less than twice as long as broad, never deep cream in colour 11
9. Leaves simple; plant rather pubescent **IV Bulbocastana** (p. 54)
   Leaves pinnate or pinnatisect; pubescence sparse or absent 10

10. Leaflets long and slender, with rounded or oblique base; stigma clavate to capitate (Bolivia)
(**S. yungasense-Commersoniana**) (p. 62)

Leaflets with cordate base, short, ovate to lanceolate; stigma saddle-shaped (Mexico)
V Cardiophylla (p. 55)

11. Leaf definitely pinnatisect (Mexico, C. America)
VI Pinnatisecta (p. 56)

Leaf definitely pinnate (S. America)
VII Commersoniana (in part) (p. 58)

12. Berries long conical or ovato-conical, more than 1½ times as long as broad 13

Berries round or only slightly oval, less than 1½ times as long as broad 14

13. Corolla lobes very short and acumens small, giving flower a ten-lobed appearance; filaments quite glabrous (Mexico) . . . **XII Demissa** (in part) (p. 68)

Corolla lobes of medium length, with well-developed acumen, or if short then filaments with well-marked pubescence (Mexico to S. America)
IX Conicibaccata (in part) (p. 63)

14. Berries ovate, with flattened apex; leaves shining, glabrescent, marginally revolute when dry; stem glabrous, or if pubescent, then with long weak spreading hairs
X Piurana (p. 66)

Plants without the above combination of characters . 15

15. Corolla with very short lobes and small acumens; lobes roughly equal in length to acumens 16

Corolla without such short lobes, rotate, pentagonal or substellate 18

16. Cultivated plants with pigmented tubers and stolons, generally tall-growing
XVII Tuberosa (in part) (p. 86)

Wild plants, generally low-growing, with unpigmented tubers and stolons or pigment only flushed over tuber, never in definite patterns 17

17. Rosette plants with the acroscopic basal lobe of each lateral leaflet better developed than the basiscopic lobe; articulation of pedicel absent or represented only by a ring of pigment . . . . **XI Acaulia** (p. 67)

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 well marked . . . . **XII Demissa** (in part) (p. 68)

18\. 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** (p. 73)

Plant without the above combination of characters . 19

19\. Corolla lobes arched; acumens large, so giving a circular appearance with acumens standing out sharply from it 20

Corolla not as above 21

20\. Leaf pinnate; interjected leaflets present (Mexico, U.S.A.) **XIII Longipedicellata** (p. 71)

Leaf pinnatisect; interjected leaflets absent; wedge-shaped wings on rhachis (S. America) **XV Cuneoalata** (in part) (p. 74)

21\. Corolla sub-stellate, the lobes broadly triangular and acumens not clearly delimited from lobes (lobes as broad as long) 22

Corolla pentagonal or rotate, not sub-stellate **XVII Tuberosa** (in part) (p. 77)

22\. Plants low-growing; terminal leaflet or lobe much larger than laterals; peduncle not bifurcate; articulation high . . . . **XVI Megistacroloba** (p. 75)

Plants without the above combination of characters . 23

23\. Plants with wedge-shaped wings on rhachis **XV Cuneoalata** (in part) (p. 74)

Plants without wedge-shaped wings on rhachis **XVII Tuberosa** (in part) (p. 77)

SERIES I *JUGLANDIFOLIA* RYDB.

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

Plants with 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 to the tomato in their morphology, differing from it in the typical

Solanum anther with no sterile tip. Distribution: mountains of Central America and north-western South America as far south as Peru. Probable centre of origin: northern South America.

KEY TO SPECIES

1. Leaf irregularly bi-pinnatisect; plant a bush, no more than 2.5 m. tall . . . . . **2. S. lycopersicoides**
   Leaf pinnate; plant a perennial woody climber (liane) much more than 2.5 m. high 2
2. Leaf rugose, hispid above; berries not more then 4.5 cm. diam. . . . . . . **1. S. juglandifolium**
   Leaf smooth, velvety; berries up to 6 cm. diam. **3. S. ochranthum**

1. S. juglandifolium Dun. (Synopsis, Montpellier, 6, 1816)

A perennial woody climber (liane); leaf pinnate, rugose and hispid above; fruit up to 4.5 cm. diam. Distribution: Costa Rica, Venezuela, Colombia, Ecuador. Forests and hedges. 2n = 24.

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

A bush or shrub, to 2.5 m. tall. Leaf bipinnatisect, very similar to that of the tomato. Distribution: Peru. Open ground. 2n = 24.

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

S. caldasii Dun. (Synopsis, Montpellier, 6, 1816)

Habit as for *S. juglandifolium*; leaf pinnate, smooth and velvety. 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 and hedges. 2n = 24.

SERIES II *ETUBEROSA* JUZ.

(Bull. Acad. Sci., U.R.S.S., **2**, 301, 1937, *nomen nudum*)

Herbs with very low almost basal pedicel articulation, but without the "bayonet hairs" typical of subsection *Basarthrum*.

The plants bear no stolons or tubers. Corolla rotate, purplish or bluish. Distribution: Central Chile as far south as the island of Chiloé; Nahuel Huapi region of S. Argentina; islands of Juan Fernandez. Probable centre of origin: Central Chile.

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 well-developed acumen, 1-2 mm. long or more 4
   Calyx with acumen completely absent or not more than 0.5-1 mm. long 3
3. Pedicel articulation 1/4 to 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, 1896; non *S. pearcei* Britton ex Rusby in Mem. Torr. Bot. Cl., *4*, 227, 1895)

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. (Linnæa, *29*, 24, 1857/8)
S. looseri Juz. (Bull. Acad. Sci. U.R.S.S., *2*, 301-2, 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. $2n = 24$.

3. S. fernandezianum Phil. (Linnæa, **29,** 23-4, 1857/8)

Plant glabrous or glabrescent; pedicel articulation right at the base. Material studied by Bukasov (1933) and Juzepczuk (1937) is reported as diploid. Distribution: Islands of Juan Fernandez. Wet forests. $2n = 24$.

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,** 13-4, 1896).
S. kunzei Phil. (Anal. Univ. Chile, Santiago, *91*, 6-7, 1896.)

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.

SERIES III *MORELLIFORMIA* HAWKES[1]

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

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[1] Herbae graciles tuberiferae, habitu plerumque epiphytico foliis simplicibus, floribus minutis atque albis et stellatis (maxima magnitudine 1.5 cm. diam.); longis ac gracilibus antheris paulum coherentibus lateraliter et baccis parvulis pauci-seminibus.

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, Wright and Hawkes, 1956). Probable centre of origin: S. Mexico.

1. S. morelliforme Bitt. et Muench (in Fedde, Repert. **12,** 154-5, 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: East and South Mexico; Guatemala. In wet mountain forests. 2n = 24.

SERIES IV *BULBOCASTANA* RYDB.

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

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. Probable centre of origin: Mexico.

Key to Species

Corolla lobes white to 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)

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

Flowers white; leaf varying from ovate to linear lanceolate according to variety. Both diploid and (apparently) autotriploid forms are known. Distribution: Central to South Mexico; Guatemala. Woods, grassland, rocks and field borders. Many forms grow under quite dry conditions at medium altitudes. 2n = 24, 36.

2. S. clarum Corr. (Texas Res. Found. Contrib., **1,** 10, 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.

SERIES V *CARDIOPHYLLA* BUK.

(ex Correll. U.S. Dept. Agr. Monogr. No. 11, 92, 1952)

Herbs with stolons and tubers, imparipinnate leaves and stellate corolla which is white or buff-coloured, sometimes tinged with purple; berries globular. Distribution: North Central to Central Mexico. Probable centre of origin: Central Mexico.

KEY TO SPECIES

1. Corolla lobes more than 5 mm. broad at the base; leaf (4-)5-7-jugate . . . . **3. S. sambucinum**
   Corolla lobes less than 5 mm. broad at the base; leaf 1-3(-4)-jugate 2
2. Anthers slender, attenuate above; calyx acumens ±1 mm. long . . . . **2. S. ehrenbergii**
   Anthers not very slender or attenuate above; calyx acumens 0.5 mm. long or shorter **1. S. cardiophyllum**

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

S. lanciforme Rydb. (Bull. Torr. Bot. Cl., *51*, 169, 1924)
S. coyoacanum Buk. (apud Rybin, Bull. Appl. Bot., *20*, 700, 1929)

Leaflets ovate-cordate, glabrous, shining, dark green above, in 3 (or 4) pairs; calyx lobes and acumens very short, the latter not more than 0.5 mm. long. Corolla buff-coloured. Anthers short, 5 mm., not attenuate above, often tinged violet inside. Both diploid and (apparently) autotriploid forms are known, the latter only occurring in the vicinity of Mexico City. Subspecies *lanceolatum*, once considered as a species (*S. lanciforme*), does not differ sufficiently from the diploid forms of *S. cardiophyllum* to be ranked as a separate species. The material mentioned in the plant breeding literature up to now as *S. lanciforme* should more correctly be considered as *S. cardiophyllum*. Distribution : Central Mexico. Dry fields, waste places and amongst rocks. 2n = 24, 36.

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

Differs from *S. cardiophyllum* by the paler green, non-shining, oblong lanceolate leaflets and the presence of hairs of varying length on leaves and stems. Calyx acumens well defined, 1 mm. long ; anthers narrow, attenuate. Petals often tinged mauve towards the tips. Mostly diploid forms are known, though a triploid (presumably autotriploid) has been recorded from San Luis Potosí : Distribution : North Central Mexico. Habitat as for *S. cardiophyllum*. Some intergrading of the two species takes place where their two distribution areas meet. 2n=24 (36).

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

Has been placed by some authors in series *Pinnatisecta* but possesses the typical calyx and pinnate leaf of *Cardiophylla*. May form a link between the two series, since it crosses with both. Agrees with *S. cardiophyllum* in the glossy dark-green leaves, but differs in the narrow lanceolate leaflets, 5-7-paired ; corolla larger, with broad triangular lobes (5-6 × 10 mm.). Distribution : N. Central Mexico, states of Querétaro and Guanajuato. Habitat as for *S. cardiophyllum*. 2n=24.

SERIES VI *PINNATISECTA* RYDB.

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

Trifida Corr. (Texas Res. Found. Contrib., **1**, 12, 1950)

Herbs with stolons and tubers, imparipinnatisect leaves and fairly large white stellate corolla. Berries globular. The division of the leaf into separate leaflets is almost complete, except for a narrow decurrent wing running along the rhachis. The two species so far investigated in the living state are diploid. Little is known yet about the six species hitherto studied as dried specimens only, and it is possible that when these are collected as living material some further taxonomic revision may be necessary. *S. trifidum* was placed by Correll in a separate series *Trifida* but seems to belong to *Pinnatisecta*. Distribution: Nicaragua and Central Mexico to Southern U.S.A. Probable centre of origin: Central Mexico.

KEY TO SPECIES

1\. Filaments united, forming a cylindrical column (Nicaragua) **6. S. nicaraguense**
Filaments free above, united below only 2
2\. Pseudostipular leaves pinnately lobed or absent, never clasping the stem 3
Pseudostipular leaves falcate or semi-lunate, clasping the stem 4
3\. Leaves glabrous; leaflets linear-lanceolate; corolla lobes only just longer than broad . **2. S. pinnatisectum**
Leaves glabrous to pubescent; leaflets ovate-lanceolate, 2.5-3 times as long as broad; corolla lobes much longer than broad . . . . **1. S. jamesii**
4\. Leaflets at least 6 times as long as broad, sub-linear, 2(-3)-jugate . . . . . . **7. S. stenophyllidium**
Leaflets 2-4 times as long as broad, ovate-lanceolate to oblong-ovate 5
5\. Lateral leaflets 1- (rarely 2-) jugate, thus the leaf generally of 3 lobes in all . . . . . **8. S. trifidum**
Lateral leaflets 2 or more-jugate 6
6\. Plant endowed with characteristic minute broadly triangular 2-celled hairs (sometimes absent from leaves and lower part of stem) . . . . **3. S. brachistotrichum**
Hairs not as described above 7
7\. Corolla with long crisp hairs on outer surface **5. S. nayaritense**
Corolla without long hairs, at most minutely puberulent **4. S. michoacanum**

1. 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 generally pubescent, occasionally glabrous, with (2)-3-4-(5)-pairs of leaflets and no interjected leaflets. Corolla lobes narrow. Distribution : N. Mexico, S.W. United States ; high mountain regions at about 2000 m. 2n = 24.

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

Distinguished from *S. jamesii* by the glabrous leaves, 5-7 leaflet pairs, generally with a few interjected leaflets and large showy corolla with broad triangular lobes. Distribution : North Central Mexico ; cultivated and arable fields, waste places and field borders. 2n = 24.

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

Distinguished from *S. jamesii* by the characteristic small triangular two-celled hairs, found at least on upper part of stem. Distribution : N. Mexico. Mountains.

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

Leaf 2-3-jugate ; stem with hairs and glands ; corolla with minute hairs only. Distribution : C. Mexico. Mountains.

5. S. nayaritense (Bitt.) Rydb. (Bull. Torr. Bot. Cl., **51**, 170, 1924)

Distinguished from the other species in this series by the long crisped hairs on the corolla. Leaf 3-4-jugate. Distribution : W. Mexico. Mountains.

6. S. nicaraguense Rydb. (Bull. Torr. Bot. Cl., **51**, 171-72, 1924)

A semi-rosette species with connate filaments. Distribution : Nicaragua.

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

Leaflets 6 times as long as broad, almost linear in shape. Distribution : W. Mexico.

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

Leaflets 1-paired (very rarely 2-paired), ovate to ovate-lanceolate in shape. Distribution : C. Mexico. Edges of pine forests.

SERIES VII *COMMERSONIANA* BUK.

(Bull. Acad. Sci. U.R.S.S., 714, 1938 ; *nomen nudum*)

Tuber-bearing herbs with imparipinnate leaves, and stellate corolla with rather broad lobes, generally less than twice as long as broad. Distribution : South America : Bolivia, Argentina, Paraguay, Uruguay, Brazil. All species so far discovered are diploid, though some autotriploid forms occur. Probable centre of origin : N.W. Argentina.

Key to Species

1. Leaflets petiolulate ; laterals ± same size as terminal ; peduncle forks not shortened 2
   Leaflets sessile or petiolulate ; laterals much shorter and/or narrower than terminal ; peduncle forks sometimes shortened considerably 4
2. Calyx acumens linear, well delimited from calyx lobes ; plant with dense pubescence of simple and glandular hairs, pleasantly aromatic . . **3. S. tarijense**
   Plant not as above 3
3. Corolla small (2 cm. diam.), with narrow lobes more than twice as long as broad, deep cream or pale yellow in colour . . . . **4. S. yungasense**
   Corolla larger, or always white, the lobes not more than twice as long as broad . . . **1. S. chacoense**
4. Lateral leaflets generally sessile ; apex of all leaflets obtuse ; peduncle forks generally reduced in length **2. S. commersonii**
   Lateral leaflets generally shortly petiolulate, with acute or even acuminate apex ; peduncle forks not reduced in length 5
5. Diameter of corolla 2 cm., leaf short (10-13 cm.), 3-jugate ; stigma short, apically notched . **5. S. acroleucum**
   Diameter of corolla 3-3.5 cm. ; leaf longer (15-18 cm.) ; stigma long ovate, apically entire . **6. S. calvescens**

1. S. chacoense Bitt. (in Fedde, Repert., **11,** 18, 1912)

S. boergeri Buk. (Rev. Argent. Agron., *4,* 239, 1937)

S. emmeae Juz. et Buk. (Bull. Acad. Sci. U.R.S.S., *2,* 321-22, 1937)

S. garciae Juz. et Buk. (Bull. Acad. Sci. U.R.S.S., *2,* 320-21, 1937)

S. gibberulosum Juz. et Buk. (Bull. Acad. Sci. U.R.S.S., *2,* 318-19, 1937)

S. guaraniticum Hassl. (Fedde, Repert., *9,* 115, 1911 ; *non* 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. *muelleri* Bitt. (in Fedde, Repert., 12, 155-56, 1913)
S. *parodii* Juz. et Buk. (Bull. Acad. Sci. U.R.S.S., *2*, 319-20, 1937)
S. *saltense* Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 113-14, 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)

Differs from S. *commersonii* in the petiolulate acuminate leaflets, the terminal leaflet hardly larger than the laterals, the uniformly white corolla and the globular berries. An extremely polymorphic species spreading through North and Central Argentine, 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 geographical sub-species, ssp. *subtilius* (based on S. *subtilius* Bitt. and including S. *jujuyense*, S. *saltense* and possibly also S. *horovitzii*), occurs in mountain valleys of N.W. Argentina at somewhat higher altitudes. Another sub-species, ssp. *muelleri*, from Argentina (Misiones) and S. Brazil, with leaflets 3 times as long as broad (based on S. *muelleri* Bitt.), can also be distinguished. A collection known to plant breeders erroneously as " S. *caldasii* " or " S. *caldasii* v. *glabrescens* " must be included as S. *chacoense*. A shorter growing sterile triploid form described as S. *millanii* has been stated to belong to S. *chacoense* but is in reality part of the S. *commersonii* complex (see below). With the exception of one certainly autotriploid collection (CPC : 1720) from Rio de la Plata, the rest of S. *chacoense* is diploid. 2n = 24 (36).

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

S. *henryi* Buk. et Lechn. (Rev. Argent. Agron., *2*, 182-3, 1935)

S. laplaticum Buk. (Rev. Argent. Agron., *4*, 238-39, 1937)
S. malmeanum Bitt. (in Fedde, Repert., *12*, 447-48, 1913)
S. mechonguense Buk. (Rev. Argent, Agron., *7*, 363, 1940)
S. mercedense Buk. (Soviet Plant Industr. Record, No. 4, 3-12, 1940)
S. millanii Buk. et Lechn. (Rev. Argent. Agron., *2*, 180-82, 1935)
S. ohrondii Carrière (Rev. Hort., *55*, 496-500, 1883)
S. pseudostipulatum (Hassl.) Buk. (Rev. Argent. Agron., *2*, 180, 1935)
S. sorianum Buk. (Soviet Plant Industr. Record, No. 4, 3-12, 1940)
S. tenue Sendt. (in Martius, Fl. Brasil., *10*, 13, 1846)

This very well-known species differs from *S. chacoense* in the leaflets which are obtusely rounded at the apex, sessile or subsessile and often slightly decurrent ; the terminal leaflet is typically much larger than the laterals and the leaf is often sublyrate in shape. Peduncle branches 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. A plexus of diploid and triploid forms from Argentina (provinces Chaco, Corrientes, Misiones), Northern Uruguay and Southern Brazil (Rio Grande) has been placed under *S. commersonii* sub-sp. *malmeanum*. It includes the former species *S. malmeanum*, *S. millanii*, and *S. pseudostipulatum*, and differs from the type in its white flowers and longer peduncle branches.

Some confusion has arisen as to the correct or typical *S. commersonii*. The type specimen collected by Commerson himself at Montevideo is probably diploid and has typical sublyrate leaves with enlarged elongated terminal leaflets and smaller decurrent laterals. This form occurs there at the present day and has been grown by the present writer (CPC 2130). The triploid forms of *S. commersonii* 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 typically *very short* peduncle branches which make the pedicels apparently spring out in a cymose umbel. This feature is seen, though not in so well marked a manner, in the diploid forms also. Distribution : East Central Argentina, Uruguay and South Brazil. Fields, waste places, woods, sandy shores. 2n = 24, 36.

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

Plant with a dense pubescence of simple and glandular hairs, pleasantly aromatic ; calyx acumens well marked, linear ; berry globular, with white raised spots. Distribution : South Bolivia (dept. Tarija) and N. Argentina (prov. Salta). Scrub and cactus vegetation in dry interandine valleys. 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,* q.v.) and may constitute a link between the two series *Commersoniana* and *Conicibaccata.* Distribution : North Bolivia, sub-tropical forests (Yungas region) at 1100-1900 m. May perhaps also be found in Peru. 2n = 24.

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

Leaf to 13 cm. long, 3-jugate ; leaflets with acute apex and short petiolules. Corolla 2 cm. diam. Distribution : Brazil, Santa Catarina.

6. S. calvescens Bitt. (in Fedde, Repert., **11,** 436-37, 1912)

Leaf larger than in *S. acroleucum.* Corolla 3-3.5 cm. diam. Distribution : Brazil ; Minas Gerais.

SERIES VIII *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 ; berries narrow-conical. Distribution : N. Bolivia ; hedges and bushy places at high altitudes. Probable centre of origin : Bolivia.

KEY TO SPECIES

1. Leaf softly hairy ; leaflets not acuminate **1. S. capsicibaccatum**
   Leaf glabrescent ; leaflets acuminate **2. S. circaeifolium**

1. S. capsicibaccatum Cardenas (Rev. Agric., Cochabamba, **2,** 35-6, 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, and grooved stigma. Distribution : Bolivia, dept. Cochabamba. 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. Sorata.

SERIES IX *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 generally purple flowers and long-conical to ovate-conical berries. Geographical distribution : Mexico, southwards to Bolivia ; all species grow in humid mountain forests.

Conicibaccata is the only taxonomic series of wild potatoes to be found both north and south of the Panamá isthmus. This is undoubtedly due to the fact that species of this series can grow in the humid forests of the Central American mountains, where apparently no other group of wild potatoes is able to exist.

The recent discovery of a polyploid series in *Conicibaccata* with diploid, tetraploid and hexaploid species is of great theoretical interest, though unfortunately no detailed cytological studies have been made on them. Probable centre of origin : Peru-Bolivia.

KEY TO SPECIES

1. Berry very long, 5-7 cm. . . . . . . **9. S. papa**
   Berry never more than 4 cm. long 2

2. Terminal leaflet both longer and much broader than laterals, which decrease in size very rapidly towards base of leaf and are 2-3-jugate (Colombia, Ecuador) . **10. S. paucijugum**
   Terminal leaflet about the same length as laterals though sometimes broader 3

3. Terminal leaflet 1½ times or more wider than laterals . 4
   Terminal leaflet less than 1½ times as wide as laterals . 5

4. Corolla stellate ; pedicel gradually swelling into calyx base ; stem generally marbled . **2. S. violaceimarmoratum**
   Corolla ± rotate ; pedicel sharply delimited from calyx base ; stem not marbled **3. S. colombianum** (ssp. *otites*)

5. Berries pointed, narrowly conical or elliptic-conical, 3-4 cm. long when mature and more than twice as long as broad 6
   Berries broadly ovato-conical with rather blunt apex, less than 3 cm. long when mature, never more than twice as long as broad 8

6. Leaf with (6-)7-9 pairs of lateral leaflets and frequent interjected leaflets . . . **6. S. agrimonifolium**
   Leaf with not more than 5 pairs of lateral leaflets and 3 pairs of interjected leaflets 7

7. Leaf with (3-)4(-5) pairs of lateral leaflets and 0-(1-2) pairs of minute interjected leaflets (Mexico and Central America) . . . . **4. S. oxycarpum**
   Leaf with 3(-5) pairs of lateral leaflets and always 2-3 pairs of conspicuous oval interjected leaflets (Peru) **7. S. buesii**

8. Whole plant covered with dense short shining pubescence ; leaf 2-(3-)-jugate . . . **11. S. urubambae**
   Pubescence not of this type 9

9. Corolla stellate or nearly so ; leaves long acuminate . 10
   Corolla ± rotate ; leaves not or only barely acuminate 11

10. Filaments pubescent ; corolla blue, 3.5-4 cm. diam. **8. S. laxissimum**

    Filaments glabrous ; corolla almost white, up to 2.2 cm. diam. . . . . **1. S. santolallae**

11. Corolla with flattened or even slightly concave lobes, appearing somewhat 10-pointed **5. S. moscopanum**

    Corolla rotate-pentagonal ; lobes not flattened or 10-pointed . . . . . **3. S. colombianum**

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

Distinguished by the more or less stellate whitish corolla, long-acuminate leaves and ovate conical berries. Distribution : S. Peru. 2n = 24.

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

Terminal leaflet much wider, though barely longer than lateral leaflets ; stem often violet-marbled ; pedicel swelling into calyx base ; corolla stellate. Distribution : N. Bolivia. 2n = 24.

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

S. dolichocarpum Bitt. (in Fedde, Repert., *12,* 4-5, 1913)

S. otites Dun. (in DC. Prodr. *13,* I. 39, 1852)

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

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

S. longiconicum Bitt. (in Fedde, Repert., *10,* 534, 1911)

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

Berries narrow-conical, 3-4 cm. long, 1-1.3 cm. wide ; leaflets acuminate ; interjected leaflets generally absent ; corolla rotate. Distribution : Mexico to Panamá (not recorded for Guatemala). 2n = 48.

5. 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. 2n = 72.

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

Leaf with (6-)7-9 pairs of leaflets and numerous interjected leaflets. Distribution : S. Mexico to Guatemala.

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

Leaf with 3(-5) pairs of lateral and 2-3 pairs of interjected leaflets. Distribution : S. Peru.

8. S. laxissimum Bitt. (Beibl. Bot. Jahrb. No. 119, **54,** 7-8, 1917)

Leaf very large ; corolla blue, 3.5 cm. diam. ; filaments pubescent. Distribution : Peru.

9. S. papa Val. (Misc. Fondo Quijano Otero, Bogotá, **16,** 1-6, 1809)

S. valenzuelae Palacio. (Mem. Mus., Paris, *2*, 340, 1816)

Berry very long (5-7 cm.). Distribution : Colombia.

10. 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 in size towards base of leaf. Berries blunt ovoid. Distribution : Colombia, Ecuador, ? Peru.

11. 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.

SERIES X *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, showy, rotate ; berry ovate, with flattened apex. Distribution : Colombia, Ecuador, N. Peru. Centre of origin probably N. Peru.

KEY TO SPECIES

1. Leaf 4-6 (-10)-jugate with 4-6 pairs of interjected leaflets **1. S. tuquerrense**

Leaf 1-3-jugate with 0-2 pairs of interjected leaflets . 2

2. Corolla not more than 2.5 cm. diam. ; leaflets lanceolate ; pedicels 3-5.5 cm. long . . . . **3. S. piurae**
Corolla 3-4 cm. diam. ; leaflets elliptic to broadly lanceolate-elliptic ; pedicels 1-2.5 cm. long 3

3. Leaf 3-jugate with 0-2 pairs of minute interjected leaflets ; filaments pubescent externally (Peru) **2. S. chomatophilum**
Leaf 1-2-jugate with no interjected leaflets ; filaments glabrous (Ecuador) . . . . **4. S. solisii**

1. 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 2-3.5 cm. diam. ; filaments glabrous. Distribution : Colombia, Ecuador. 2n = 48.

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

Leaf 3-jugate with 0-4 pairs of small interjected leaflets ; leaflets elliptic or broad lanceolate-elliptic, corolla 4 cm. diam. with short lobes ; filaments pubescent externally. Distribution : N. Peru.

3. S. piurae Bitt. (Beibl. Bot. Jahrb., No. 119, **54**, 5-6, 1917)

Leaf 2-3(-4)-jugate ; 1-3 pairs of interjected leaflets ; leaflets lanceolate ; pedicels 3-5.5 cm. long ; corolla to 2.5 cm. diam. ; filaments glabrous. Distribution : N. Peru.

4. 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 to 3.5 cm. diam. ; filaments glabrous. Distribution : Ecuador.

SERIES XI *ACAULIA* JUZ.

(Bull. Acad. Sci. U.R.S.S., **2**, 316, 1937 ; *nomen nudum*)

Low rosette-forming herbs, 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 : Central Peru, Bolivia and N.W. Argentina at very high altitudes (±4000 m.) in alpine meadows, field borders, etc. Probable centre of origin : S. Bolivia to N.W. Argentina.

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

S. aemulans Bitt. et Wittm. (Bot. Jahrb., *50*, 553-55, 1914)

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

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

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, *S. acaule*. The species name "*S. schreiteri*" found in the Russian literature has not been given a description, but specimens received under that name should certainly be included under *S. acaule*. 2n = 48.

SERIES XII *DEMISSA* BUK.

(Bull. Acad. Sci. U.R.S.S., 715, 1938 ; *nomen nudum*)

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. Probable centre of origin: Central Mexico.

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 8

2\. Berries elongate-conical or pointed-oval ; frequent . 3
Berries round ; frequent or rarely produced . . 5

3\. Flowers very large (3-4 cm. diam.) ; plant erect ; leaf straight, 4-6-jugate ; lateral leaflets with 0-3 pairs of interjected leaflets . . . . **8. S. iopetalum**
Flowers smaller (2-3 cm. diam.) ; leaf type various . 4

4. Leaf well-dissected, with 5 pairs of laterals and up to 8 or more pairs of interjected leaflets **6. S. guerreroense**
Leaf poorly dissected, with 2-3 pairs of laterals and 0-3 pairs of interjected leaflets . . **4. S. brachycarpum**

5. Lateral leaflets sessile or sub-sessile; terminal leaflets larger than laterals; peduncle short 6
Lateral leaflets petiolulate; terminal leaflets about the same size as laterals; peduncle longer 7

6. Pubescence of leaf coarse, white, easily visible to the naked eye; stem always well-developed; berries rare or none . . . . . **3. S. × semidemissum**
Pubescence not easily visible; stem poorly developed or if long showing several inflorescences from the base upwards; berries frequent . . **5. S. demissum**

7. 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 . **3. S. × semidemissum**

8. Corolla lobes rounded, fruits white-verrucose
1. S. verrucosum
Corolla lobes flat and sloping 9

9. Corolla white, sometimes with purple splashes; acumens rather large; plant tall . . . **7. S. spectabile**
Corolla purple; acumen smaller; plant dwarf
5. S. demissum (aberrant form)

1. S. verrucosum Schlechtd. (Hort. Halensis, **1**, 3, 1841)

S. squamulosum Mart. et Gal. (Bull. Acad. Brux., *12*, 1, 140, 1845)

Distinguished by the 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 of all *Demissa* species contributing the one genome that they seem to possess in common. It constitutes a link with series *Tuberosa* and is indeed difficult to separate from it. Distribution: Central to South Mexico in Pine and *Abies* forests, perhaps at not such high levels as *S. demissum*. $2n = 24$.

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

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

Includes all forms that have arisen as hybrids between *S. tuberosum* and *S. demissum.* The name *S. salamanii* was applied to naturally occurring hybrids between *S. demissum* and *S. tuberosum* subsp. *andigena.* Distribution: Central Mexico; weed of cultivated ground and field borders. 2n = 60.

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

Differs from *S. demissum* in the stalked leaflets and from *S. edinense* in the 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 more probably by a *S. demissum* × *S. stoloniferum* cross. No berries. Distribution: C. Mexico; field weed or along hedges and waysides, sometimes in woods. 2n = 60.

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

Distinguished from *S. demissum* by the conical berries, non-rosette habit and petiolulate acuminate leaflets. Distribution: West Central Mexico; high pine forests. 2n = 72.

5. 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 or sub-sessile with rounded apex. Berries round (longer in v. *longibaccatum*). Distribution: Mexico, from Durango State southwards into Guatemala; high pine forests. 2n = 72.

(*Note.*—An aberrant form with sloping corolla lobes (CPC 1342) needs further taxonomic investigation.)

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

Distinguished from *S. demissum* by the conical fruits and from *S. brachycarpum* by the well-dissected leaves with 5 pairs of primary laterals and 8 or more pairs of interjected leaflets. Distribution : S.W. Mexico, in high altitude pine-oak forests. 2n = 72.

7. S. spectabile (Corr.) Hawkes (Ann. Mag. Nat. Hist., Ser. 12, **7**, 701-02, 1954)

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

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

This species, based on Bitter's *S. verrucosum* var. *iopetalum*, differs from *S. verrucosum* in the larger more rotate corolla, conical smooth berries and long leaves. Distribution : Mexico, Hidalgo State.

SERIES XIII *LONGIPEDICELLATA* BUK.

(Bull. Acad. Sci. U.R.S.S., 715, 1938 ; *nomen nudum*)

Herbs with long creeping stolons ; leaves with coarse white hairs. The arched corolla lobes and large acumens give the corolla a circular appearance with acumens standing out sharply from it. Distribution : Central Mexico to S.W. United States on dry plateaux and mountain slopes, medium altitudes. Probable centre of origin : C. Mexico.

KEY TO SPECIES

1. Pedicel very densely clothed with white spreading hairs, even above the articulation . . **3. S. polytrichon**
Pedicel sparsely hairy to almost glabrous, especially above the articulation ; if densely pubescent below articulation then hairs adpressed 2

2\. Corolla almost circular in outline, except for the sharply delimited acumens; leaflets acuminate 3

Corolla not as above; lobes ± broadly triangular and gradually passing into the acumens; leaflets obtuse or acute, not or only slightly acuminate **2. S. fendleri**

3\. Corolla dark purple; terminal leaflet broadly obovate to rhomboid . . . . **1. S. × vallis-mexici**

Corolla white to medium purple; terminal leaflet not differing greatly from laterals. **4. S. stoloniferum**

1. 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 that is larger than the laterals. Formed probably as a hybrid between *S. stoloniferum* (2n = 48) and *S. verrucosum* (2n = 24), occurring in the valley of Mexico where the altitude ranges of these two species overlap. 2n=36.

2. 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)

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

Leaflets not acuminate; corolla acumens large, not so sharply delimited from the lobes as in the typical members of the series; pedicel sparsely pubescent. Distribution: North Central Mexico (San Luis Potosi) northwards to Arizona, New Mexico, Texas and Colorado. 2n = 48.

3. S. polytrichon Rydb. (Bull. Torr. Bot. Cl., **51,** 150, 1924)

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, the white corolla and generally high articulation. Some forms have sparse leaf pubescence, but the spreading pedicel pubescence is a constant feature.[1] Distribution: North Central Mexico to N. Mexico (Querétaro to Chihuahua States). 2n=48.

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[1] White-flowered forms known to potato 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 based on white-flowered forms described by Asa Gray under *S. fendleri*, which Bitter himself had not seen. The name *S. boreale* is thus a *nomen dubium*, and its use should therefore be discontinued.

4. S. stoloniferum Schlechtd. (Linnæa, **8**, 255, 1833)

- *S. ajuscoense* Buk. (apud Rybin, Bull. Appl. Bot., *20*, 609-700, 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, dry plateaux, valleys and hillsides, chiefly as ruderal plants. 2n = 48.

SERIES XIV *POLYADENIA* BUK.

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

Tuber-bearing herbs with very dense indumentum of glandular hairs of an objectionable odour ; corolla white, pentagonal to sub-stellate. Berries are rather cordate, flattened, with black streaks, especially on the edges. Distribution : Central Mexico, on dry stony hillsides, amongst walls, etc. Centre of origin : Mexico.

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

Characters and distribution as for series. A certain amount of variation, chiefly in leaf dissection, exists in natural populations. 2n = 24.

SERIES XV *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, substellate 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. Probable centre of origin: S. Bolivia-N. Argentina.

KEY TO SPECIES

1. All leaf lobes linear; leaf small . . **2. S. xerophyllum**
   At least the terminal leaf lobe not linear, generally long-lanceolate, leaf larger . . **1. S. infundibuliforme**

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

Leaflets roughly lanceolate or linear-lanceolate. Interjected leaflets entirely absent. A form from the Argentine-Bolivian border previously classed as *S. platypterum* owing to the very wide rhachis wings is probably not sufficiently distinct to be given specific rank; similarly with *S. glanduliferum* which bears glands on the leaves. Distribution: Central Bolivia to N.W. Argentina and N. Chile; dry cactus and scrub deserts. 2n = 24.

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

S. microphyllum Hawkes. (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 118, 1944; *non S. microphyllum* Dun., Hist. Solan. 187, 1813)
S. pinnatifidum Cardenas. (Rev. Agric., Cochabamba, *2*, 33-4, 1944; *non S. pinnatifidum* Ruiz et Pav., Flora Peruv., *2*, 37, 1798-1802)

Leaf to 5 cm. long, much smaller than that of *S. infundibuliforme*; leaflets ± linear to 1.2 cm. long. Distribution: C. Bolivia to N. Argentina.

SERIES XVI *MEGISTACROLOBA* CARD. ET 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 articulation very high ; corolla substellate, purple. Distribution : S. Peru to N.W. Argentina, growing in waste places, open mountain pastures, etc. Probable centre of origin : N.W. Argentina.

KEY TO SPECIES

1. Terminal leaflet and minute laterals (if present) definitely acuminate . . . . **3. S. sanctae-rosae**
   Terminal leaflet and minute laterals (if present) obtuse or acute, never acuminate 2
2. Leaf simple (never with more than 1 minute pair of lobes at base of terminal leaflet) 3
   Leaf with well-developed lateral lobes or leaflets . . . 5
3. Leaf oblong-elliptic, rather sharply truncate at base **5. S. ellipsifolium**
   Leaf rhomboid, ovate or spathulate, cuneate at base . 4
4. Leaf ± ovate to rhomboid . **1. S. megistacrolobum**
   Leaf long-spathulate or very long obovate **4. S. toralapanum**
5. Decurrent portions of lateral lobes or leaflets rather narrow and short 6
   Decurrent portions of lateral lobes or leaflets very broadly triangular, running down rhachis for a considerable way 7
6. Terminal leaflet broadly ovate-orbicular, blunt or mucronate at apex . . . . . **2. S. raphanifolium**
   Terminal leaflet long ovate to obovate, long ellipsoid or rhomboid . . . . **1. S. megistacrolobum**

7. Lateral leaflets only slightly smaller than terminal, interjected leaflets present (2-3 pairs) . **6. S. hawkesii**

Lateral leaflets much smaller than terminal; interjected leaflets absent (or never more than 1) **4. S. toralapanum**

1. 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: N. Bolivia to N.W. Argentina, high altitude plateaux and hillsides. $2n = 24$.

2. S. raphanifolium Card. et Hawkes (J. Linn. Soc., Bot., **53**, 94-5, 1945)

Distinguished from *S. megistacrolobum* chiefly by the broadly ovate-orbicular terminal leaflet and the paler more rotate corolla. Distribution: S. Peru; waste places, hillsides, etc. $2n = 24$.

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

Distinguished from the two previous species 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. $2n=24$.

4. S. toralapanum Card. et Hawkes (J. Linn. Soc., Bot., **53**, 98-9, 1945)

S. decurrentilobum Card et Hawkes (J. Linn. Soc., Bot., *53*, 97-8, 1945)

Distinguished from the preceding 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. 2n = 24.

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

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

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

Distinguished from the 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.

SERIES XVII *TUBEROSA* RYDB.

(Bull. Torr. Bot. Cl., **51**, 146-48, 1924)

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 characterized by imparipinnate or simple leaves, general absence of glandular pubescence, 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 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 both wild and cultivated species. There is also an additional key to the cultivated potatoes on p. 86, which may be referred to if it is already known that the species in question is cultivated.

Presence of pink or red pigmentation in the flowers and/or tubers and a definite pattern on the tubers are two indications of cultigens, though some escaped forms of *S. tuberosum* lack these features.

Mistakes made in the key to the series on p. 48 may be rectified in the *Tuberosa* key since the reader is referred back to other series where appropriate.

KEY TO WILD AND CULTIVATED SPECIES

(Key to Cultivated Species only on p. 86)

1. Anthers and stamens not well demarcated, the yellow anther pigment suffusing down on to the filament; flowers white (Chile, W. Argentina) . . **9. S. maglia**
   Anthers and filaments quite distinct, both in form and colouration 2
2. Leaf simple, or with one or two minute lateral lobes only 3
   Leaf with quite visible and well-developed lateral leaflets 7
3. Articulation very high (only 2-3 mm. below calyx base); flowers purple, sub-stellate; plants small, ± rosette-forming . . . . (see **Megistacroloba,** p. 75)
   Articulation lower, or if high then not combined with the other characters noted above 4
4. Calyx lobes and acumens linear-lanceolate, 5-12 mm. long; stem with no wings; fls. white (C. Peru) **26. S. hypacrarthrum**
   Calyx lobes and acumens not more than 5 mm. long; stem with or without wings; fls. white or purple . . 5
5. Plant short, rosette-forming or sometimes with a short stem; fls. purple (C. Bolivia) . **3. S. boliviense**
   Plant generally with well-developed stems; flowers white (Bolivia-N. Argentina) 6
6. Plant slender (sometimes rosette-forming at high altitudes, 3800-4000 m.); stem without wings or if present very narrow and straight **17. S. simplicifolium** (ssp. **microdontum**)
   Plant robust; stem with well-developed wings which are marginally crisped . . **17. S. simplicifolium**

7. Corolla sub-stellate, *i.e.*, the length of each lobe about equal to the breadth, and the "shoulders" poorly developed 8
Corolla pentagonal or rotate, the lobes having distinct "shoulders" and well differentiated acumens . . 17

8. Pedicel articulated at or near the base, never above the centre 14
Pedicel articulated at or above the centre . . . 9

9. Pedicel articulation very high; plants growing in ± rosettes; terminal lobe of leaf much larger than laterals; broadly decurrent leaflet wings on rhachis (see **Megistacroloba,** p. 75)
Plant not possessing the above characteristics . . 10

10. Plant with a dense indumentum of glandular hairs of varying lengths; corolla pale blue-violet (Bolivia) **2. S. berthaultii**
Plant with no glandular pubescence 11

11. Leaflets 3-5 times as long as broad, acuminate; corolla generally white (N. Argentine) **16. S.×setulosistylum**
Leaflets not more than 2½ times as long as broad; corolla blue-purple 12

12. Leaflets about 2½ × as long as broad (N. Argentina) **5. S. gourlayi**
Leaflets about 2 × as long as broad 13

13. Interjected leaflets 0-2-paired (see **Longipedicellata,** *S. fendleri*, p. 72)
Interjected leaflets very frequent . **22. S. sucrense**

14. Stigma very small, not thicker than style apex; plant in a rosette or semi-rosette; terminal leaflet often 3-lobed; fls. blue (S. Bolivia, N.W. Argentina) **14. S. oplocense**
Plant without this combination of characters . . 15

15. Hairs on leaflet margins thick and easily visible without a lens; leaflets broad ovate, not more than 3 times as long as broad (N.W. Argentina) **S.×velascanum** (see p. 101)
Hairs absent or inconspicuous on leaflet edges; leaflets narrow-ovate to narrow-elliptic, 3-5 times as long as broad 16

16. Leaf hairs inconspicuous; corolla markedly sub-stellate (N.W. Argentina) . . . **25. S × famatinae**
Leaf hairs very thick, short and conspicuous; corolla almost pentagonal . . **8. S. leptophyes** (in part)

17. Calyx acumens very long, lanceolate to linear, sometimes even subspathulate, 5-12 mm. × 1-1.5 mm.; calyx itself often with long dense coarse hairs, or with small stalked glands 18
Calyx acumens not of this type, or if so, then the pubescence is normal and sparse 22

18. Leaf 1-3-jugate; pubescence not glandular . . 20
Leaf 6 or more-jugate; pubescence sometimes glandular 19

19. Pubescence glandular or absent (Peruvian coast) **21. S. wittmackii**
Pubescence normal (Peruvian mountains) **33. S. multiinterruptum**

20. Leaf 1-2-jugate; terminal leaflet much broader than laterals, oblong to broadly elliptic or suborbicular; stigma bilobed (C. Peruvian coast and mountains) **11. S. medians**
Leaf 2-3-jugate; terminal leaflet not much broader than laterals; stigma entire 21

21. Lateral leaflets oblong-lanceolate, broadly decurrent on to rhachis for some distance (S. Peruvian mountains) **36. S. sandemanii**
Lateral leaflets ovate-lanceolate, not or only slightly decurrent on to rhachis (S. Peruvian coast) **39. S. weberbaueri**

22. Leaf poorly dissected, without more than 1-3(4) pairs of lateral leaflets which are smaller than terminal and decrease rapidly in size to base of leaf 23
Leaf well dissected, with 4-6 or more pairs of lateral leaflets, or if only 3 at least 2 of these pairs of approximately same size as terminal 38

23. Flowers white 24
Flowers deep purple, blue, pale violet or pink . . 28

24. Calyx lobes and acumens linear-lanceolate, 5-12 mm. long; stem wingless (Peru) . . **26. S. hypacrarthrum**
Calyx lobes and acumens much smaller, wings present; or if very much reduced then calyx acumens short, 1-4 mm. 25

25. Stems strongly winged, the wings crisped marginally; plant robust 26
Stems with barely developed wing; plant slender . 27

26. Calyx acumens 3-5 mm. long ; wild plants with velvety pubescent leaf and tubers with long dormancy period (S. Bolivia, N.W. Argentina) . **17. S. simplicifolium**
Calyx acumens 1-2 mm. long ; cultivated plants with shiny leaf and no tuber dormancy (Colombia to Bolivia)
42. S. phureja (some forms)

27. Rhachis and petioles winged ; leaf margins smooth (N.) Argentina) . . . . . . **S. bijugum** (see p. 101)
Rhachis and petioles not winged ; leaf margins minutely toothed (Bolivia, N. Argentina)
17. S. simplicifolium (ssp. **microdontum**)

28. Flower pink (cultivated species with no tuber dormancy (Colombia to Bolivia) . **42. S. phureja** (in part)
Flower blue, violet, mauve, etc. 29

29. Leaflet apex very long and attenuated in upper leaves ; lateral leaflets 1(-2)-jugate (C. Peru)
S. acroglossum (see p. 101)
Leaflet apex not so long ; lateral leaflets (2-)3 or more-jugate 30

30. Leaves, calyx and pedicels very densely covered with acute, not very long hairs 31
Calyx and pedicels sparsely pubescent 32

31. Hairs white . . . . . **34. S. pillahuatense**
Hairs yellowish . . . . **37. S. villuspetala**

32. Margins of corolla lobes rolled inwards ; berries verrucose, with white raised spots (Mexico)
(see **DEMISSA.** *S. verrucosum*, p. 69)
Margins of corolla lobes not rolled inwards ; berry without raised white spots (S. America) 33

33. Upper lateral leaflets very widely decurrent on to rhachis, the wing being almost as broad above as its length
(see **Megistacroloba,** p. 75)
Upper lateral leaflets not or only very slightly decurrent ; rhachis without a broadly triangular wing . . 34

34. Lateral leaflets petiolulate 35
Lateral leaflets sessile 36

35. Stem wingless ; plant slender (wild species)
38. S. virgultorum
Stem winged ; plant robust (weed species)
S. sparsipilum (some forms)

36. Plant in a rosette; interjected leaflets absent (Peru) . . . **35. S. pumilum**

Plant not in a rosette, occasional interjected leaflets formed 37

37. Leaflets with well-marked acuminate apex (Colombia, Ecuador) . . . . **1. S. andreanum**

Leaflets with obtuse apex (Bolivia) . **23. S. brevicaule**

38. Stem, leaf and calyx glabrous (perhaps a few minute 1-celled hairs and glands visible under a strong lens); fls. white; calyx lobes and acumens short (Peru) . 39

Stem, leaf and calyx with some 2 or more-celled hairs. 40

39. Leaflets linear-lanceolate, 4-5 times as long as broad **6. S. gracilifrons**

Leaflets broad-lanceolate, 2½-3½ times as long as broad . **27. S. immite**

40. Stem with ± dense long spreading hairs; pedicel articulated near the apex, 4-6 mm. long above the articulation 41

Stem without long spreading hairs; pedicel articulation not so high 44

41. Interjected leaflets frequent, 10-25 pairs or more (Peru) . 42

Interjected leaflets few, sub-orbicular, small (0-4 pairs) 43

42. Lateral leaflets ovate, terminal sub-orbicular . **12. S. multidissectum**

Lateral and terminal leaflets oblong-elliptic **13. S. neohawkesii**

43. Plant growing in a low rosette; calyx small, 3-5 mm. long; no glandular hairs on plant (Colombia) **30. S. lobbianum**

Plant with well-developed stem; calyx large, 8-10 mm. long; glandular hairs frequent over leaves and stems (Peru) . . . . **15. S. pampasense**

44. Leaflets of lowest leaves narrow, at least 4 times as long as broad, ± lanceolate or linear-lanceolate 45

Leaflets of lowest leaves broader, less than 4 times as long as broad 46

45. Stem woody below, unwinged, terete, covered with dense short velvety pubescence; flowers yellowish-white (Peru) . . **28. S. lignicaule**

Stem winged or angled, not endowed with pubescence as above; fls. purple, large (Bolivia) . . **24. S. candolleanum**

46. Calyx irregular, bilabiate, with sepals in groups of 2 + 3 or 2 + 2 + 1, generally large and prominent . . 47

Calyx regular, the sepals not in groups . . . 52

47. Plant with delicate leaves, not more than 10 cm. long; hairs on upper leaf surface overlapping; flowers large (3-4 cm. diam.), pale blue (wild species; Peru) **18. S. soukupii**

Plant with larger leaves, more than 10 cm. long, or if less, then hairs on upper leaf surface not overlapping, flowers of various colours, not or seldom larger than 3-3.5 cm. diam. (cultivated and weed species) . . . 48

48. Calyx small (5-7 mm. long); leaflets broad-ovate, twice as long as broad (weed species) **19. S. sparsipilum** (some forms)

Calyx larger, generally 9-11 mm. long or even longer . 49

49. Leaflets about twice as long as broad; under-surface of leaf with dense white silky hairs (wild species) **32. S. multiflorae**

Leaflets narrower; hairs not dense white or silky (cultivated species) 50

50. Lobes of corolla 3 times as broad as long, the width generally more than the corolla radius; corolla "shoulders" square and well-marked; plants tall and vigorous (Peru, Bolivia). . . **44. S. × chaucha**

Lobes of corolla less than 3 times as broad as long, the width considerably less or only just equalling the corolla radius; corolla "shoulders" rounded . . . 51

51. Leaf sparsely pubescent, shining in the living state; tubers yielding in 3-4 months under 12-hour day-length and having no dormancy period (Venezuela to Bolivia) **42. 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 well-marked dormancy period (Peru, Bolivia) . . . **.43. S. stenotomum**

52. Pedicel articulation below centre, sometimes quite close to base; leaflet edges provided with thick short hairs visible without lens; corolla white or with purple streaks on under-surface (W.-N.W. Argentina) **7. S. kurtzianum**

Pedicel articulation, at or above centre; leaflet edges without hairs as mentioned above 53

53. Pedicel articulation very high, over 3/4 of length above base, 2-4(-6) mm. below calyx base; young plant often forming a rosette (cultivated species) . . . 54
Pedicel articulation lower, generally about centre or 2/3 length above the base; young plant not rosette-forming 58

54. Corolla roughly pentagonal in outline (though "shoulders" quite evident); leaves softly hairy; upper lateral leaflets broadly decurrent on to rhachis (Bolivia and possibly Peru) . . . . . **40. S. ajanhuiri**
Plants without the above characteristics 55

55. Corolla rotate to pentagonal; leaves not in a pronounced rosette at base of plant
46. S. tuberosum (aberrant forms)
Corolla rotate with very short lobes; leaves in a fairly well-marked rosette at base of plant . . . 56

56. Pedicels indistinctly articulated; corolla blue, not more than 25 mm. diam., common peduncle short, 2-4 cm. long . . . . . . **45. S. × juzepczukii**
Pedicels distincly articulated; corolla purple, 30-35 mm. diam.; common peduncle longer, 5-10 cm. or more . 57

57. Stigma bilobed or notched apically; tubers white or dark purple (cultivated sp., S. America)
47. S. × curtilobum
Stigma simple; tubers flushed red-purple, or whitish. (weed sp., Mexico)
(see **DEMISSA:** *S × edinense*, p. 70)

58. Upper lateral leaflets more than 2½ times as long as broad 59
Upper lateral leaflets 2½ times as long as broad or less 63

59. Leaves 3-jugate, whitish below, shining above; interjected leaflets 0-2 paired, minute (Peru)
10. S. marinasense
Leaves more than 3-jugate, not whitish below; interjected leaflets generally more frequent 60

60. Calyx acumens 2-4 mm. long; leaf with adpressed silky pubescence; interjected leaflets numerous (Peru)
4. S. canasense
Calyx acumens shorter 1-1.5 mm. (Bolivia, N. Argentina 61

61. Upper lateral leaflets small, 1.5-2.5 cm. long
8. S. leptophyes
Upper lateral leaflets much larger, 3-5 cm. long . . 62

62. Corolla pale purple ; leaf pubescence sparse
31. S. mollepujroense
Corolla deep purple ; leaf pubescence dense
29. S. liriunianum

63. Leaf with 2-4 pairs of lateral leaflets and few interjected leaflets 64
Leaf with more than 4 pairs of lateral leaflets and many interjected leaflets 66

64. Peduncle, pedicels and calyx covered with a dense white weft of hairs ; no interjected leaflets
34. S. pillahuatense
Hairs on peduncle pedicels and calyx not as above ; interjected leaflets nearly always present . . . 65

65. Plants rather low growing ; flowers always blue ; weed plants with long stolons and colourless tubers (diploids)
19. S. sparsipilum
Plant vigorous ; flowers blue, blue-purple, red-purple or white ; cultivated plants with shorter stolons and coloured tubers (tetraploids)[1]. . **46. S. tuberosum**

66. Lower surface of leaf clothed with dense white woolly pubescence ; corolla large, dark purple (Argentina)
20. S. vernei
Lower surface of leaf not clothed with dense white pubescence ; corolla of varying size and colour . 67

67. Stem glabrescent ; calyx small, about 5 mm. long ; peduncle very long, 16 cm. (Peru)
33. S. multiinterruptum
Stem pubescent ; calyx 7-11 mm. long or more
46. S. tuberosum

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[1] Weed or escaped forms of *S. tuberosum* with blue flowers can be distinguished from *S. sparsipilum* by the large number of interjected leaflets (5-12 pairs per leaf).

KEY TO CULTIVATED SPECIES

1\. Articulation of pedicel high, 2-4(-6) mm. below calyx base, always more than 3/4 length of pedicel; leaves stiff, not arched at tip 2

Articulation lower, not more than 2/3 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 . . **40. 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 . . . . **45. S. × juzepczukii**

Pedicels distinctly articulated; corolla purple, 3-3.5 cm. diam.; common peduncle longer, 5-10 cm. or more long . . . . **47. S. × curtilobum**

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

Calyx lobes short, oblong or short ovate-triangular, generally regularly arranged . . . **46. S. tuberosum**

5\. Lobes of corolla 3 × as broad as long, generally broader than the corolla radius . . . . **44. 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 . . . . . **42. 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 **43. S. stenotomum**

WILD SPECIES

1. 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 rather acuminate leaflets and purple rotate corolla. Distribution: Colombia, Ecuador. Damp high altitude woods and bushy places. 2n = 24.

2. S. berthaultii Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 122, 1944)

Very glandular species with pale blue-violet corolla, pentagonal to semi-rotate. It may form a link between series *Tuberosa* and *S. tarijense* in series *Commersoniana*. Distribution: Central Bolivia (dept. Cochabamba). Dry scrubby places. 2n = 24.

3. 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. Dry scrubby places and cultivated fields. 2n = 24.

4. 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. Distribution: S. Peru. Dry stony places. 2n = 24.

5. 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 slightly decurrent; terminal leaflet broader than laterals, flowers pale purple, semi-stellate. Distribution: N.W. Argentina. Dry hillsides amongst cactus and scrub vegetation at high altitudes. 2n = 24.

6.* S. gracilifrons Bitt. (Beibl. Bot. Jahrb., No. 119, **54,** 6-7, 1917)

Distinguished by very numerous narrow leaflets with minute sparse hairs and white corolla. Possibly related to *S. lignicaule*. Distribution: C. Peru, dept. Huancavelica. Dry savannas. 2n = 24.

7. S. kurtzianum Bitt. et Wittm. (Bot. Jahrb., **50**, Suppl., 548-50, 1914)

S. macolae Buk. (Rev. Argent. Agron., *4*, 239-40, 1937)

Distinguished by the elliptic-obtuse 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 rotate, white or with central petal streak of bright violet on external surface only. Distribution: Argentina (provinces Mendoza to Catamarca) on dry bushy hillsides. 2n = 24.

8. S. leptophyes Bitt. (in Fedde, Repert., **12**, 448-49, 1913)

S. pachytrichum Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 121-22, 1944)

S. spegazzinii Bitt. (in Fedde, Repert., *12*, 449-50, 1913)

A low-growing slender species with narrow-lanceolate leaflets 3-4 times as long as broad. Corolla pentagonal, tending towards sub-stellate at the southern part of its range, due probably to introgression from *S. chacoense*. Leaf dissection is not as intense generally as with *S. canasense*. *S. leptophyes* is morphologically similar to some forms of the cultivated species *S. stenotomum*, with which it may perhaps have some affinities. Distribution: South Peru, Bolivia and N.W. Argentina, as far south as Tucumán and Catamarca. Dry open places or amongst scrub. 2n = 24.

9. 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, etc.; Argentina, province Mendoza. 2n = 24, 36.

10.* S. marinasense Vargas (Publ. Univ. Nac. Cuzco, **1**, 83-5, 1949, *nomen nudum*)

Distinguished by the leaves which are bright and shining above, paler and dull below, 2-3 pairs of broadly lanceolate leaflets. Flower blue, very showy. A very distinct species. Distribution: S. Peru. Dry grassy hillsides. 2n = 24.

11. 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. simplicifolium* 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. Distribution: C. Peru, coastal belt and lower altitudes, in dry desert or scrub vegetation. 2n = 24, 36. The forms with 36 chromosomes possess almost orbicular leaves and 0-1 pairs of interjecteds. The diploids possess narrower leaflets and more laterals; the name *S. neoweberbaueri* was probably applied to these diploid forms, whilst the triploids were given the name *S. medians.* Since the triploids are almost certainly auto-triploids the two are here grouped together under the first validly published name: *S. medians.*

12. 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 and from *S. neohawkesii* in the ovate (not oblong) leaflets and other characters. Distribution: Central to South Peru; common at high altitudes in grass, amongst rocks and in field borders. 2n = 24.

13. S. neohawkesii Ochoa (Rev. Argent. Agron., **19,** 231-34, 1952)

Plant forming a basal rosette at first. Leaf highly dissected with 6-8 pairs of primary lateral leaflets and numerous interjecteds; with dense long hairs on stem, leaf rhachis, peduncles, etc. Differs from *S. multidissectum* in the oblong-ovate leaflets, larger more purple flower, etc. Distribution: Central Peru at high altitudes in alpine meadows, waste places, etc. 2n = 24. (This species seems to possess affinities with *S. multiinterruptum* and *S. bukasovii* Juz. (see p. 101), but further material is needed before we can say whether it is conspecific with them).

14. S. oplocense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 119, 1944)

A low rosette-forming species with short broad leaves and leaflets which are covered with rather dense coarse hairs. Corolla semi-stellate; stigma very minute. Distribution: S. Bolivia, possibly spreading into N.W. Argentina. Dry inter-andine valleys in desert scrub and cactus vegetation. 2n = 24.

15. S. pampasense Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 125, 1944)

Semi-rosette habit with lanceolate leaflets covered with hairs of varying lengths, most gland-tipped. Flower pale purple to pale blue; anthers long and narrow. Distinguished from other species by the peculiar pubescence. Distribution: Central Peru (depts. Ayacucho and Apurimac) at low altitudes (2000 m.) in subtropical dry inter-andine valleys. 2n = 24.

16. S. × setulosistylum Bitt. (in Fedde, Repert., **12**, 450-52, 1913)

Vegetatively similar to *S. chacoense* but with coarser hairs and white stellate corolla often tinted with mauve. Style setae sometimes present. This name has been given to hybrid populations derived apparently from natural crosses between *S. chacoense* and *S. leptophyes*. Distribution: N.W. Argentina, scrub and waste land at fairly low altitudes, 1900-2650 m. 2n = 24.

17. S. simplicifolium Bitt. (in Fedde, Repert., **11**, 369-70, 1912)

S. gigantophyllum Bitt. (in Fedde, Repert., *11*, 368-69, 1912).

S. microdontum Bitt.[1] (in Fedde, Repert., *10*, 535-36, 1912)

Large straggling plants with generally winged stems, large ovate simple leaves or often with 1-2(-3) pairs of lateral leaflets

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[1] Although the name *S. microdontum* takes priority over *S. simplicifolium* it is not as yet sufficiently well studied for us to be quite certain that the two species are synonymous. In order to avoid unnecessary nomenclatural changes I have retained the name *S. simplicifolium* for the time being, therefore, until living material of *S. microdontum* becomes available for study.

as well. Corolla white, rotate. Distribution: the typical form occurs in S. Bolivia and N.W. Argentina from about 1000-2500 m. in forests and on path-sides. Subspecies *microdontum* is a low-altitude more delicate form from Argentina, province Salta (± 1400 m.), whilst subspecies *venturii* (ined.) is a high-altitude delicate, wingless and often semi-rosette form from Argentina, provinces Tucumán and Catamarca, whose altitude ranges from about 2000-3200 m. 2n = 24.

18. S. soukupii Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 122-23, 1944)

Rather similar to *S. leptophyes* in habit, with small leaves and narrowly lanceolate leaflets. Differs, however, in the very large flowers, 3-4.5 cm. diam., and rounded corolla lobes with rather small acumen. May possibly be a derivative of *S. leptophyes*. Distribution: South Peru, Dept. Puno. High altitude waste places and scrub-covered hillsides. 2n = 24.

19. S. sparsipilum (Bitt.) Juz. et Buk. (in Vavilov, Theor. Bases Plant Breed., **3**, 11, 1937)

S. *anomalocalyx* Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 126-27, 1944)
S. *aracc-papa* Juz. (Bull. Acad. Sci. U.R.S.S., **2**, 306-07, 1937)
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. *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 rôle in the evolution of some of the cultivated potato species (Hawkes, 1956). Distribution: Central Peru, southwards to Central Bolivia. Cultivated fields, waysides and waste places. 2n = 24.

20. S. vernei Bitt. et Wittm. (Bot. Jahrb., **50,** Suppl., 550-51, 1914)

S. *ballsii* Hawkes (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 121, 1944)

A tall robust plant with large leaves and 4-6 pairs of ovate or ovate-lanceolate leaves covered below with a white cottony or woolly pubescence. Flowers deep purple, often very large. Subsp. *ballsii* (based on S. *ballsii*) is a northern form of this species with sessile leaflets and rather smaller flowers. It is doubtful whether S. *vernei* has played any part in the formation of cultivated potato species. Distribution: North-West Argentina, provs. Jujuy, Salta, Tucumán, Catamarca. Damp woods and waysides. 2n = 24.

21.* S. wittmackii Bitt. (in Fedde, Repert., **12,** 54-6, 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 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.

According to Bukasov (1938, 1941) *S. wittmackii* is a tetraploid (2n = 48), whilst the forms known to me in a living state are certainly diploid (2n = 24). Possibly an autotetraploid race of this species exists?

22. 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 substellate 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, dept. Chuquisaca. An arable and garden weed, also found in waste places. 2n = 48.

23. 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.

24. S. candolleanum Berth. (Ann. Sci. Agron., Paris, **2**, 185, 1911)

S. mandoni 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-jugate narrow lateral leaflets and numerous interjected leaflets; calyx lobes lanceolate. Distribution: N. Bolivia, dept. La Paz.

25. S × famatinae Bitt. et Wittm. (Bot. Jahrb., **50**, Suppl., 552-53, 1914)

Leaf similar to *S. chacoense* ssp. *subtilius*; pedicel articulation low; corolla substellate, purple. Probably a hybrid of *S. kurtzianum* and *S. chacoense*. Distribution: N.W. Argentina, provs. La Rioja, Catamarca.

26.* 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. This species should possibly be included in Series *Piurana*. Distribution: C. Peru, dept. Lima.

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

S. mathewsii Bitt. (in Fedde, Repert., *12*, 53-4, 1913)

Leaf glabrous, rather similar to that of *S. chacoense*; corolla large, white, rotate, very showy. Distribution: Central Peru, dept. Lima.

28.* S. lignicaule Vargas. (Rev. Argent. Agron., **10,** 398, 1943)
S. vargasii Hawkes. (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 113, 1944)

Stem terete, with velvety pubescence; stem and leaf yellow-green. Corolla yellowish white. A very distinct species of unknown affinities. Distribution: South Peru, dept. Cuzco.

29. S. liriunianum Card. et Hawkes. (J. Linn. Soc., Bot., **53,** 106-08, 1945)

Leaflets narrow, with whitish pubescence; pedicels to 3.5 cm. long; corolla dark purple. Is possibly related to *S. vernei*. Distribution: Bolivia, dept. Cochabamba.

30. S. lobbianum Bitt. (in Fedde, Repert., **12,** 446-47, 1913)

Stem very short; leaf long and narrow; stem and peduncle with long spreading hairs similar to those of *S. neohawkesii* and *S. multidissectum*, to which latter species *S. lobbianum* may be related. Distribution: S. Colombia; exact locality not recorded.

31. S. mollepujroense Card. et Hawkes. (J. Linn. Soc., Bot., **53,** 103-104, 1945)

Has affinities with *S. sparsipilum*, but differs in the lanceolate leaflets and glabrescent leaf surface. Distribution: Bolivia, dept. Cochabamba.

32.* S. multiflorae Vargas. (Publ. Univ. Nac. Cuzco, **1,** 93-5, 1949; *nomen nudum*)

A very curious species with perhaps some affinities to *S. urubambae*. Calyx bilabiate; corolla acumens long. Distribution: S. Peru, dept. Cuzco.

33. S. multiinterruptum Bitt. (in Fedde, Repert., **12,** 56-7, 1913)

Probably related to *S. neohawkesii*, but differs in the absence of long spreading hairs on the stem, the very long peduncle, and broad obovate-elliptic lateral leaflets in only 5 pairs. Distribution: C. Peru, dept. Lima.

34.* S. pillahuatense Vargas. (Publ. Univ. Nac. Cuzco, **1,** 90-91, 1949; *nomen nudum*)

Peduncles and pedicels with spreading short white hairs; leaf small; leaflets 2-jugate. A distinct species of unknown affinities. Distribution: S. Peru, dept. Cuzco.

35. S. pumilum Hawkes. (Bull. Imp. Bur. Plant Breed. & Genet., Cambridge, 124, 1944)

Plant with basal leaf rosette and very long peduncle (7 cm.); rhomboid terminal leaflet much larger than the 2-3-jugate laterals. Distribution: S. Peru, dept. Cuzco.

36. S. sandemanii Hawkes. (Ann. Mag. Nat. Hist., Ser. 12, **7,** 709-10, 1954)

Leaf imparipinnatisect; laterals 2-3-jugate, the upper pair decurrent; no interjecteds; calyx lobes often sub-spathulate, very pubescent; corolla bright violet. Distribution: S. Peru, dept. Arequipa.

37.* S. villuspetala Vargas. (Publ. Univ. Nac. Cuzco, **1,** 92-93, 1949; *nomen nudum*)

Leaf 1-2-jugate, covered with very dense silky yellowish hairs. A curious species similar to *S. caripense* (non-tuber-bearing) except for the high pedicel articulation. (? tuberiferous.) Distribution: S. Peru, dept. Cuzco.

38. S. virgultorum (Bitt.) Card. et Hawkes. (J. Linn. Soc., Bot., **53,** 103, 1945)

Rather similar to *S. simplicifolium* ssp. *microdontum* but with blue flowers and growing at much higher altitudes. Distribution : N. Bolivia, dept. La Paz.

39. S. weberbaueri Bitt. (in Fedde, Repert., **11,** 365-66, 1912)

Related to *S. medians* and *S. sandemanii*, but differs from the former in the narrower less decurrent leaflets and from the latter in the presence of interjected leaflets and more numerous laterals. Distribution : S. Peru, dept. Arequipa.

CULTIVATED SPECIES

40. 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 involving also the triploid species *S. juzepczukii* (see below). Frost resistant. Distribution : N. Bolivia, dept. La Paz, at high altitudes. 2n = 24.

41. 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 northern derivative of *S. stenotomum* with large white or pink flowers and ribbed calyx base. Tubers with bright yellow flesh. Forms with pinkish-lilac flowers occur both in *S. stenotomum* and *S. goniocalyx* and were formerly grouped by me as a distinct species *S. yabari*. In view of the fact that this colour has now been found to be due only to a single gene difference (Dodds and Long, 1955) the species *S. yabari* cannot be maintained as distinct. It is possible also that *S. goniocalyx* may also be shown to be an extreme variant of *S. stenotomum*, but since the evidence available so far is not very conclusive it seems better to retain it for the present. Distribution : Central Peru, dept. Junín. 2n = 24.

42. 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. 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 at lower altitudes than the other cultivated species so far described. $2n = 24$.

43. 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 lanceolate lobes as in *S. phureja*. A very variable species which is probably ancestral to all the other cultivated potatoes. These have been produced from it either by hybridization (*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. goniocalyx*, *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*. Distribution: South Peru to Central Bolivia at very high altitudes. Some forms are frost resistant. 2n = 24.

44. S. × chaucha Juz. et Buk. (Proc. U.S.S.R. Congr. Genet., **3**, 609, 1929)

S. chocclo Juz. et Buk. (in Vavilov, Theor. Bases Plant Breed., *3*, 18, 1937, *nomen nudum*)
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*. 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 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*[1] 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. Distribution: Central Peru to Central Bolivia. 2n = 36.

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[1] Bukasov (1939) considers that *S.* × *chaucha* was derived from *S. phureja*. From morphological and genetical evidence I consider this to be very unlikely.

45. 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* 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. $2n = 36$.

46. S. tuberosum L. (Sp. Pl. 1, 185, 1753)

S. andigena[1] Juz. et Buk. (Proc. U.S.S.R. Congr. Genet., *3*, 609-10, 1929)
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. herrerae Juz. (Bull. Acad. Sci. U.R.S.S., *2*, 310-11, 1937)
S. leptostigma Juz. (Bull. Acad. Sci. U.R.S.S., *2*, 309-10, 1937)
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)
S. subandigena Hawkes (Imp. Bur. Plant Breed. & Genet., Cambridge, 128, 1944)

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, never narrow lanceolate as in some forms of *S. stenotomum* and *S. phureja*. Corolla lobes

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[1] Formerly written as *S. andigenum*; orthography revised according to Index Kewensis.

about half as long as broad. Tubers with well-marked dormancy period.

Two subspecies are now recognized (Hawkes, 1956) :—

(i) Subsp. **andigena** (Juz. et Buk.) Hawkes (based on *S. andigena* Juz. et Buk.) from the Andes of Venezuela, Colombia, Ecuador, Peru, Bolivia and N.W. Argentina. This is distinguished by narrower leaflets, leaves set at acute angle to stem, generally more dissected; pedicel not thickened at apex; tubers formed only at high altitudes[1] (over 2000 m.) under short-day conditions. This is undoubtedly the ancestral subspecies of *S. tuberosum*, formed either partly or wholly from *S. stenotomum* in the Andes of Peru and Bolivia. Escaped forms maintaining themselves as weeds have been described under the names of *S. herrerae* (Peru) and *S. subandigena* (Bolivia). They differ only in the longer stolons and unpigmented tubers from the cultivated varieties.

(ii) Subsp. **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. Pedicels thickened above; corolla often white or pale coloured. Tubers formed under long days or under short days in the tropics only at lower altitudes (500-2000 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). Chromosome numbers of all forms: 2n = 48.

47. 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

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[1] They are, of course, formed under experimental conditions in Europe at low altitudes, but not in the tropics where the temperatures are very high.

30-35 mm. diam. with very short lobes and acumens. Derived from natural crosses between *S.* × *juzepczukii* and *S. tuberosum* subsp. *andigena*. Numerous variations in tuber colour and form are known. Central Peru to South Bolivia at high altitudes. Frost resistant. 2n = 60.

APPENDIX

Species whose taxonomic position is in some doubt, due in some cases to unavailability of photographs, type specimens or adequate descriptions, are listed below :—

> *S. abbotianum* Juz., *S. acroglossum* Juz., *S. acroscopicum* Ochoa, *S. ambosinum* Ochoa, *S. bijugum* Bitt., *S. boreale* (A. Gray) Bitt., *S. bukasovii* Juz., *S. caniarense* Juz. et Buk., *S. cayeuxii* Berth., *S. chiquidenum* Ochoa, *S. confusum* Corr., *S. cuencanum* Juz. et Buk., *S. jalcae* Ochoa, *S. leptosepalum* corr., *S. raquialatum* Ochoa, *S. rhomboideilanceolatum* Ochoa, *S. riobambense* Juz. et Buk., *S. schenkii* Bitt., *S. schizostigma* Bitt., *S. sogarandinum* Ochoa, *S. tacnaense* Ochoa, *S. velascanum* Bitt. et Wittm.

" Species " names that have appeared in the recent literature without any description (" *nomina nuda* ")[1] are given below, together with affinities where known. Their use should be discontinued unless valid descriptions are later published :—

> *S. antipochacoense* (see Koopmans, 1951), *S. antipophureja* (see Koopmans, 1951), *S. artificiale* (see Toxopeus, 1947), *S. catamarcae* (? =*S. sanctae-rosae*), *S. ciezae*, *S. chuga*, *S. dolichostigma* (=*S. chacoense*), *S. demissorosum* (see Koopmans, 1951), *S. erlansonii*, *S. fonckii* (=*S. tuberosum*), *S. gandarae* (=*S. stoloniferum*), *S. kaufmanii* (? =*S. sparsipilum*), *S. macmillanii*, *S. martinezii* (=*S. stoloniferum*), *S. maydiforme*, *S. mendozinum* (=*S. kurtzianum*), *S. pauciflorum*, *S. reddickii* (=*S. stoloniferum*), *S. rionegrinum* (=*S. commersonii*), *S. ruderale* (? =*S. sparsipilum*), *S. schreiteri* (=*S. acaule*), *S. tarmense* (=*S. tuberosum* subsp. *andigena*), *S. triferum* (? =*S. phureja*), *S. venezuelicum* (? =*S. colombianum*).

[1] Some species in Series Tuberosa (see pp. 88, 94) described by Dr Vargas were not validated by a latin description and are technically *nomina nuda*, although adequate descriptions in Spanish were given. I have considered them of sufficient interest, however, to include in the main text, and it is to be hoped that latin descriptions will be published at a later date. The same also applies to a number of cultivated species described (in Russian) by Dr S. M. Bukasov in Vavilov, Theoretical Bases of Plant Breeding, *3*, 1937, the taxonomic position of some of which is not clear to me.

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ALPHABETICAL LIST OF LATIN NAMES OF SERIES AND SPECIES

(Series in capitals. Synonyms, homonyms and *nomina nuda* in italics; no names of authorities are given with *nomina nuda*, for which no adequate vernacular descriptions exist.)

PAGE

S. abbottianum Juz. 101
S. acaule Bitt. 68
ACAULIA Juz. 67
S. acroglossum Juz. 101
S. acroleucum Bitt. 62
S. acroscopicum Ochoa 101
S. aemulans Bitt. et Wittm. 68
S. agrimonifolium Rydb. 66
S. ajanhuiri Juz. et Buk. 95
S. ajuscoense Buk. 73
S. alpicum Standl. et Steyerm. 70
S. alticola Bitt. 76
S. ambosinum Ochoa 101
S. andigena Juz. et Buk. 98
S. andreanum Baker 86
S. anomalocalyx Hawkes 91
S. antipochacoense 101
S. antipophureja 101
S. antipoviczii Buk. 73
S. aracc-papa Juz. 91
S. artificiale 101
S. ascasabii Hawkes 96
S. ballsii Hawkes 92
S. berthaultii Hawkes 87
S. bijugum Bitt. 101
S. boergeri Buk. 59
S. boliviense Dun. 87
S. boreale (A. Gray) Bitt. 72, 101
S. boyacense Juz. et Buk. 96
S. brachistotrichum (Bitt.) Rydb. 58
S. brachycarpum Corr. 70
S. brevicaule Bitt. 93
S. brevidens Phil. 52
S. brevimucronatum Hawkes 91
S. buesii Vargas 66
S. bukasovii Juz. 101
BULBOCASTANA Rydb. 54
S. bulbocastanum Dun. 54
S. bustillosii Phil. 53
S. calcense Hawkes 91
S. caldasii Dun. 51, 52, 60
S. calvescens Bitt. 62
S. canasense Hawkes 87
S. candelarianum Buk. 73
S. candolleanum Berth. 93
S. caniarense Juz. et Buk. 101

PAGE

S. capsicibaccatum Card. 63
S. cardenasii Hawkes 96
CARDIOPHYLLA Buk. 55
S. cardiophyllum Lindl. 55
S. catamarcae 101
S. catarthrum Juz. 91
S. cayeuxii Berth. 101
S. chacoense Bitt. 59
S. chaucha Juz. et Buk. 97
S. chiloense (A. DC.) Berth. 98
S. chiquidenum Ochoa 101
S. chocclo Juz. et Buk. 97
S. chomatophilum Bitt. 67
S. chuga 101
S. churuspi Hawkes 96
S. ciezae 101
CIRCAEIFOLIA 62
S. circaeifolium Bitt. 63
S. clarum Corr. 55
S. coeruleiflorum Hawkes 97
S. collinum Dun. 88
S. colombianum Dun. 65
COMMERSONIANA Buk. 58
S. commersonii Dun. 60
S. confusum Corr. 101
CONICIBACCATA Bitt. 63
S. coyoacanum Buk. 55
S. cuencanum Juz. et Buk. 101
S. cultum (A. DC.) Berth. 98
CUNEOALATA Hawkes 74
S. curtilobum Juz. et Buk. 99
S. decurrentilobum Card. et Hawkes 76
DEMISSA Buk. 68
S. demissorosum 101
S. demissum Lindl. 70
S. depexum Juz. 68
S. dolichocarpum Bitt. 65
S. dolichocremastrum Bitt. 66
S. dolichostigma 101
S. edinense Berth. 70
S. ehrenbergii (Bitt.) Rydb. 56
S. ellipsifolium Card. et Hawkes 77
S. emmeae Juz. et Buk. 59
S. erlansonii 101
S. esculentum Neck. 98
ETUBEROSA Juz. 51
S. etuberosum Lindl. 53
S. famatinae Bitt. et Wittm. 93
S. fendleri A. Gray 72
S. fernandezianum Phil. 53
S. flahaultii Bitt. 66
S. fonckii 101
S. fragariaefructum Hawkes 91
S. gandarae 101
S. garciae Juz. et Buk. 59
S. gibberulosum Juz. et Buk. 59

PAGE

S. gigantophyllum Bitt. 90
S. glanduliferum Hawkes 74
S. goniocalyx Juz. et Buk. 95
S. gourlayi Hawkes 87
S. gracilifrons Bitt. 87
S. guaraniticum Hassl. 59
S. guerreroense Corr. 71
S. hawkesii Card. 77
S. henryi Buk. et Lechn. 60
S. herrerae Juz. 98
S. horovitzii Buk. 60
S. hypacrarthrum Bitt. 93
S. immite Dun. 93
S. infundibuliforme Phil. 74
S. iopetalum (Bitt.) Hawkes 71
S. jalcae Ochoa 101
S. jamesii Torr. 58
JUGLANDIFOLIA Rydb. 50
S. juglandifolium Dun. 51
S. jujuyense Hawkes 60
S. juzepczukii Buk. 98
S. kaufmanii 101
S. kesselbrenneri Juz. et Buk. 96
S. knappei Juz. et Buk. 60
S. kunzei Phil. 53
S. kurtzianum Bitt. et Wittm. 88
S. lanciforme (Bitt.) Rydb. 55
S. lapazense Hawkes 91
S. laplaticum Buk. 61
S. laxissimum Bitt. 66
S. lechnoviczii Hawkes 87
S. leptophyes Bitt. 88
S. leptosepalum Corr. 101
S. leptostigma Juz. 98
S. lignicaule Vargas 94
S. liriunianum Card. et Hawkes 94
S. lobbianum Bitt. 94
S. longiconicum Bitt. 65
LONGIPEDICELLATA Buk. 71
S. longipedicellatum Bitt. 73
S. longistylum Corr. 54
S. looseri Juz. 53
S. lycopersiciodes Dun. 51
S. macolae Buk. 88
S. macmillanii 101
S. maglia Schlechtd 88
S. malinchense Hawkes 73
S. malmeanum Bitt. 61
S. mamilliferum Juz. et Buk. 97
S. mandoni A.DC. 93
S. manoteranthum Bitt. 65
S. marinasense Vargas 88
S. martinezii 101
S. mathewsii Bitt. 93
S. maydiforme 101
S. mechonguense Buk. 61

PAGE

S. medians Bitt. 89
MEGISTACROLOBA Card. et Hawkes 75
S. megistacrolobum Bitt. 76
S. mendozinum 101
S. mercedense Buk. 61
S. michoacanum (Bitt.) Rydb. 58
S. microdontum Bitt. 90
S. microphyllum Hawkes 74
S. millanii Buk. et Lechn. 61
S. molinae Juz. 98
S. mollepujroense Card. et Hawkes 94
S. morelliforme Bitt. et Muench 54
MORELLIFORMIA Hawkes 53
S. moscopanum Hawkes 66
S. muelleri Bitt. 60
S. multidissectum Hawkes 89
S. multiflorae Vargas 94
S. multiinterruptum Bitt. 94
S. nannodes Corr. 72
S. nayaritense (Bitt.) Rydb. 58
S. neo-antipoviczii Buk. 73
S. neo-hawkesii Ochoa 89
S. neo-weberbaueri Wittm. 89
S. nicaraguense Rydb. 58
S. ochranthum Dun. 51
S. ohrondii Carr. 61
S. oplocense Hawkes 90
S. otites Dun. 65
OXYCARPA Rydb. 63
S. oxycarpum Schiede 65
S. pachytrichum Hawkes 88
S. palustre Poepp. 53
S. pampasense Hawkes 90
S. papa Val. 66
S. papita Rydb. 72
S. parodii Juz. et Buk. 60
S. pauciflorum 101
S. paucijugum Bitt. 66
S. pearcei Phil 52
S. phureja Juz. et Buk. 96
S. pichinchense Bitt. et Sodiro 86
S. pillahuatense Vargas 94
S. pinnatifidum Card. 74
PINNATISECTA 56
S. pinnatisectum Dun. 58
S. piurae Bitt. 67
PIURANA Hawkes 66
S. platypterum Hawkes 74
POLYADENIA Buk. 73
S. polyadenium Greenm. 74
S. polytrichon Rydb. 72
S. pseudostipulatum (Hassl.) Buk. 61
S. pumilum Hawkes 94
S. punae Juz. 68
S. punoense Hawkes 91
S. raphanifolium Card. et Hawkes 76

PAGE
S. raquialatum Ochoa 101
S. reddickii 101
S. rhomboideilanceolatum Ochoa 101
S. riobambense Juz. et Buk. 101
S. rionegrinum 101
S. rybinii Juz. et Buk. 96
S. ruderale 101
S. sabinii (A. DC.) Berth. 98
S. salamanii Hawkes 70
S. saltense Hawkes 60
S. sambucinum Rydb. 56
S. sanctae-rosae Hawkes 76
S. sandemanii Hawkes 94
S. santolallae Vargas 65
S. schenckii Bitt. 101
S. schickii Juz. et Buk. 60
S. schizostigma Bitt. 101
S. schreiteri 68, 101
S. semidemissum Juz. 70
S. setulosistylum Bitt. 90
S. simplicifolium Bitt. 90
S. sinense Blanco 98
S. sogarandinum Ochoa 101
S. solisii Hawkes 67
S. sorianum Buk. 61
S. soukupii Hawkes 91
S. sparsipilum (Bitt.) Juz. et Buk. 91
S. spectabile (Corr.) Hawkes 71
S. spegazzinii Bitt. 88
S. squamulosum Mart. et Gal. 69
S. stenophyllidium Bitt. 58
S. stenotomum Juz. et Buk. 96
S. stoloniferum Schlechtd. 73
S. subandigena Hawkes 98
S. subandinum Meigen 53
S. subtilius Bitt. 60
S. sucrense Hawkes 93
S. tacnaense Ochoa 101
S. tarijense Hawkes 62
S. tarmense 101
S. tenue Sendt. 61
S. tenuifilamentum Juz. et Buk. 97
S. tilcarense Hawkes 76
S. tlaxcalense Hawkes 73
S. toralapanum Card. et Hawkes 76
S. triferum 101
TRIFIDA Corr. 56
S. trifidum Corr. 58
TUBEROSA Rydb. 77
S. tuberosum L. 98
S. tuquerrense Hawkes 67
S. urubambae Juz. 66
S. utile Klotzsch 70
S. valenzuelae Pal 66
S. vallis-mexici Juz. 72
S. vargasii Hawkes 94

PAGE

S. vavilovii Juz. et Buk. 92
S. velascanum Bitt. et Wittm. 101
S. venezuelicum 101
S. vernei Bitt. et Wittm. 92
S. verrucosum Schlechtd. 69
S. villuspetala Vargas 94
S. violaceimarmoratum Bitt. 65
S. virgultorum (Bitt.) Card. et Hawkes 95
S. weberbaueri Bitt. 95
S. wightianum Rydb. 72
S. wittmackii Bitt. 92
S. xerophyllum Hawkes 74
S. yabari Hawkes 95, 96
S. yungasense Hawkes 62

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