CHROMOSOME NUMBERS IN ASTRAGALUS AND OXYTROPIS WITH A DISCUSSION ON THE PHYLOGENY OF THESE GENERA

A

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CHROMOSOME NUMBERS IN ASTRAGALUS AND OXYTROPIS WITH A DISCUSSION ON THE PHYLOGENY OF THESE GENERA

INTRODUCTION

Man has always been interested in the identification of plants and animals. At first, this interest was confined to the plants and animals which could be used as sources of food. Later, the medicinal properties of plants were discovered and utilized. Finally, people started to classify plants and animals because of the intrinsic interest of the subject itself.

For many hundreds of years, the science of taxonomy has been developing. With the adoption of the Linnaean binomial nomenclature, a major step was taken toward the unification of classification systems. However, the morphological characters which are the basis of classical taxonomy show an almost unbelievable diversity within species, depending on individual heredity and environment. Because of this diversity, identification by individual taxonomists varies considerably. It would thus seem logical to search for a character or characters which would be subject to less diversity than factors such as plant height, flower color and leaf shape.

This is the point at which the experimental taxonomist can be of value. There are several methods used by experimental taxonomists, which, when employed with the methods of the classical taxonomist, could lead to a better taxonomy.

The chromosome number of a plant or animal is usually characteristic of the species. This character is being employed more widely in taxonomic work. The stability of the chromosome number would appear to make it of value in taxonomic and evolutionary studies. Chromosome numbers have been used in the analysis of such genera as Drosophila (Patterson and Stone, 1952) and Nicotiana (Goodspeed, 1954).

Another method used by experimental taxonomists employs biochemistry. Attempts to classify species within genera by biochemical analysis have met with some success in the last few years. Workers at Rutgers University such as H. D. Hammond (1947, 1952) and M. A. Johnson (1954) have carried out serological investigations using precipitin tests to separate species. More recently, paper chromatography has been widely employed in taxonomic investigations. Alston and Irwin (1961) and Riley and Bryant (1961) have used "secondary compounds" such as phenolics and pigments in the chromatographic analysis of plants. This group of compounds appears to be the most specific for botanical chromatography. The refinement of biochemical methods will undoubtedly result in providing a most useful tool for taxonomists in future years.

Most biologists agree that taxonomy should reflect phylogeny. In this thesis an attempt has been made to test the reliability of the chromosome number as a morphological character for the separation of species and genera in the legume family. Chromosome numbers have then been linked with geographic distribution in an attempt to determine the phylogeny of two genera, Astragalus and Oxytropis.

Previous investigations of chromosome numbers in the genus Astragalus had shown a base number of $n = 8$ for Old World species (Senn, 1938; Darlington and Wylie, 1955) and $n = 11$, 12 or 13 in New World species (Anderson, 1940; Vilkomerson, 1943; James, 1951; Turner, 1956; Head, 1957; Ledingham, 1957). This information led to the postulation (Ledingham, 1960) that Old World and New World species belonged to two different evolutionary lines which, perhaps, warranted the distinction of two separate genera. If, however, there had been a common origin of Old and New World groups, a reduction in chromosome number from n = 12 appeared the most likely explanation for the existing situation. These ideas were based on 200 chromosome counts of _Astragalus_ and the closely related genus _Oxytropis_ which has a base number of 8.

According to Lemée (Good, 1953), _Astragalus_, with an estimated 2000 species, is the largest genus of flowering plants. It was decided that since only one tenth of the total number of species had been counted, a better understanding of the phylogeny of the group would be possible if more counts were known. If the distinction in chromosome number between the two groups remained, then further support for the separation of the genus would result. If intermediate numbers, 9's or 10's were found, the theory of a common origin with a reduction in chromosome number would seem more likely.

The short time alloted for this research, as well as the large size of the genus, prohibited a complete cytological examination of the known species. For this study, material was requested from areas in the Near East, Southern Russia, Southern and Central Europe and Egypt. Because of the large number of species and the great morphological variation of the species, this part of the world was considered particularly favorable for study. A great number of sections with no previous counts had representative species in this area. This suggested a possibility of finding cytological variation in some of the species selected for study. The assurance of assistance from Dr. K. H. Rechinger of the Natural History Museum, Vienna, in obtaining identified material from collections in the Near East made the project feasible.

Further contacts made during 1960 and 1961 made possible the extension of the study area.

TECHNIQUE

Mitotic counts were made in the genus *Astragalus* by the following method. The seeds were scarified and germinated between filter papers in petri dishes. The young seedlings were taken when the primary root tip was 1 to 2 cm. long and placed in a 0.002 mol. solution (0.058 gm. in 200 cc. of distilled water) of 8 - hydroxyquinoline at 15 - 17°C. for 8 - 12 hours. This treatment, which caused a shortening of the chromosomes and an apparent separation, facilitated counting. Fixation was in Carnoy's solution (3:1 - Absol. :HAc) for 15 - 20 minutes. The seedlings were then transferred to 70% alcohol and stored in the refrigerator.

The best stain was obtained using a normal procedure for the Feulgen technique with a 10 minute hydrolysis in 1N HCl at 60°C. The seedlings were placed in the stain for one to two hours before squashing. No decolorizing was necessary. About 3 mm. of the root tip was teased out on a slide which had been acid cleaned overnight to facilitate adhesion of the material to the slide and hence minimize the losses of material that are often incurred during preparation of permanent slides. A drop of distilled water was put on the material and the coverslip was then placed at a 45° angle over the material so that the corners protruded at the top and bottom of the slide. The slide was then placed between paper towels and tapped firmly with the end of a blunt stick. Sometimes a very slight heating of the slide facilitated squashing. Caution had to be exercised if this step was included because excess heat caused decolorization of the Feulgen stain. The degree of staining could be controlled to some extent. If the material was pale, addition of water under the coverslip resulted in a deepening of the stain when allowed to sit for 15 to 20 minutes. Dilute HAc added under the coverslip caused the removal of most of the excess stain when the material was too dark.

To make a permanent mount, a slide was placed with the coverslip down on a piece of dry ice. When the coverslip was frozen to the slide, (ca. 2 minutes), the coverslip was flicked off with a quick tap on one of the extended corners. The slide was then taken through an "Up" alcohol series from 40% to Absolute. Diaphane was used as the mounting material. New coverslips were used for the permanent mounts. This method was learned from Dr. J. M. Naylor of the Field Husbandry Department, University of Saskatchewan.

Division figures were located on the permanent slides. An average of ten counts was taken to give a good chromosome count on a new species. More than one slide was always made to determine that the count was representative of the sample. Camera lucida drawings were made for all new species counts.

In a number of species, tetraploid cells were observed to occur in the same root tip with the diploid cells. In all cases, the lower number has been reported.

Whenever enough seed material was available, seedlings were planted in the greenhouse at the Regina Campus of the University of Saskatchewan. Some of the species proved to be short-lived annuals which completed flowering and fruiting in the greenhouse. However, most of the plants were transferred to the garden after they had become established. At the time of writing, many of the plants had not yet flowered. It is hoped that a complete set of voucher specimens will be deposited in the herbarium at the University of Saskatchewan, Regina Campus.

There is no monograph on the genus *Astragalus*. The study of the habitat and geographical distribution of the species counted has been considered a rather important factor in this study. In most cases the information was obtained from available floras of specific regions. The search for this material involved the investigation of an extensive literature, as indicated by the titles cited in the bibliography.

RESULTS

A total of 100 counts in two genera of the Leguminosae is reported here. These include 84 new counts (72 of *Astragalus* species and 12 of *Oxytropis* species), and 16 counts (15 of *Astragalus* species and 1 of an *Oxytropis* species), which had previous published counts. Three of the latter counts differed from the previous reported counts. A diploid number of 2n = 16 was found for *A. campylorrhynchus* Fisch. et Mey. In 1935, Tschechow reported this species as having n = 18. *A. campylotrichus* Bge. was found to have 2n = 16, whereas Tschechow had reported n = 16. *Oxytropis sulphurea* (Fisch.) Ldb. had a number of 2n = 16. Ledingham had reported a count of 2n = 48 in his 1960 paper. The reason for the discrepancies in these counts is not known. The counts for *A. campylotrichus* could possibly be due to the occurrence of a tetraploid race. Diploid numbers of 16 and 48 as reported in

O. sulphurea are not easy to accept. This is not the only case, however, where such a condition exists. Chromosome counts of 2n = 32 and 2n = 48 have been made for A. campestris (L.)DC. In the latter case, the plants on which these differing counts were made have been identified as the same species. Perhaps situations such as the two mentioned here are worthy of fuller examination.

Eight more counts have been made on Astragalus species from Iraq and Armenia. These counts are being withheld until positive identification of the species has been made.

An attempt was made to germinate almost all of the seed samples which were received of species that had no previous published counts. A large number of the seed samples received contained immature or parasitized seed, and therefore yielded no chromosome counts.

The genus Oxytropis is included in this discussion because of its very close relationship to Astragalus. Some taxonomists include Oxytropis as a subgenus under Astragalus. Often the growth habits and morphological characteristics of the two genera intergrade. A biochemical analysis of these two groups would seem, from preliminary work done during this study, to support the continued separation of these genera. However, the fact that the names are used interchangeably in some floras necessitates the inclusion of Oxytropis with Astragalus at this time.

Table I summarizes the chromosome numbers in Astragalus and Oxytropis which are reported in this thesis for the first time. A brief description of the habitats of the species is given in the final column. The ideas about habitat changes which may have occurred during the evolution of these genera have been derived from a study of the present habitats. These ideas are included in the discussion.

The only new count obtained which deviated from the usual base number of 8 in the Old World was that for A. ugamicus M.Pop.. The somatic number of 2n = 82 appears to have no clear derivation. Further seed obtained from the original source did not germinate, therefore no confirmation of this count was possible. The only possible explanation of this count is that an increase in number took place from a deciploid 2n = 80. Another species, A. bucesas, appears to have a diploid number of 40 to 44. This count is only approximate and no official record is made of it on the species list. If the counts of these two species can be finalized, and if they remain as they are thought to be at this time, some connection with a base number of 10 would be a possible explanation.

One species counted, A. römeri Simk., had an unusually high number of chromosomes. This high number of chromosomes made it extremely difficult to obtain an accurate count. A large number of cells showed over 100 chromosomes. The best cell for counting gave a number of 169 chromosomes. This count has been recorded as an approximate number. It is the largest count ever reported in the genus Astragalus. In the graphs, this count makes up the column listed as greater than 48.

TABLE I

Chromosome numbers in Astragalus and Oxytropis for which there are no previous published counts.

Species	Section	2n	Fig.	Map	Seed Source	Habitat
*A. ackerbergensis Freyn.	Proselius	32	21	24	Ashkhabad #540, U.S.S.R.	Mountains 1500-1600 m.
*A. aksuense Bge.	Cenanthrum	16	33	36	Leningrad, U.S.S.R.	Light woodlands, subalpine meadows
*A. alexandrinus Boiss.	Myobrama	16	6	17	Cairo, Egypt	Sandy places
*A. alopecias Pall.	Alopecias	16	54	23	Taschkent #542, U.S.S.R.	Sandy places, wormwood deserts, River banks
*A. amalecitanus Boiss.	Ammodendron	16	70	72	Jerusalem, Israel	Calcareous stony hills
*A. andreji Rzazade		16	32	35	Baku, U.S.S.R.	
*A. bombycinus Boiss.	Platyglottis	16	4	14	Cairo, Egypt Haines, 20/4/55, Iraq	Compact sandy soil
A. brachypetalus Trautv.	Stereothrix	16	20	26	Ashkhabad #542, U.S.S.R.	Mountain slopes with couchgrass and wormwood
*A. bungei C. Winkl. et Fedtsch.	Platyglottis	32	66	67	Taschkent #478, U.S.S.R.	Mountain slopes
*A. coluteocarpus Boiss.	Coluteocarpus	16	45	47	Taschkent, U.S.S.R.	Banks of mountains, rivers, river valleys
*A. corrugatus Bert. =A. kotschyanus Boiss.	Harpilobus	32	8	8	Rec.8664, Iraq	Sandy soils, uncultivated fields

TABLE I (cont'd)

Species	Section	2n	Fig.	Map	Seed Source	Habitat
*A. cottenianus Aitch. et Baker	Proselius	16	62	63	Taschkent #481, U.S.S.R.	Mountains on clay and sand-stone slopes
A. eremospartoides Rgl.	Corethrum	16	49	50	Taschkent, U.S.S.R.	Sandy places of foothills
*A. eximius Bge.	Alopecias	16	57	58	Taschkent, U.S.S.R.	Stony slopes of mountains at 2800 m.
*A. expansus Boiss.	Onobrychium	16	36	39	Riga, U.S.S.R.	Calcareous hills near deserts
*A. finitimus Bge.	Alopecias	16	9	6	Rech. 9682, Iraq	Prairie foothills and dry slopes
*A. globiceps Bge.	Harpilobus	48	15	18	Rech. 9587, Iraq Rech. 9539, Iraq	Sandy compact soil
A. heterodontus Boriss	Brachycarpus	16	18	21	Leningrad, U.S.S.R.	At levels of 3400-3500 m., on river banks and lake shores
*A. hispidulus DC.	Ankylotus	16	3	12	Cairo, Egypt	Deserts
*A. hissaricus Lipsky	Proselius	16	56	57	Taschkent, U.S.S.R.	Light soils on mountain slopes in ephemerid veg.
*A. hypoleucus Schauer	Micranthi	28	89	88	Univ. of Mich. U.S.A.	Gravelly mesas among pines and junipers. Lower T.L.Z.
*A. illyricus Bernh.	Proselius	16	39	42	Zagreb, Yugoslavia	
*A. interpositus Boriss	Onobrychium	16	28	31	Baku, U.S.S.R.	Upper prairies, limestone slopes of gorges

TABLE I (cont'd)

Species	Section	2n	Fig.	Map	Seed Source	Habitat
*A. iskanderi Lipsky	Xiphidium	16	58	59	Taschkent, U.S.S.R.	Mixed grassland steppes, middle mountain districts
*A. kahiricus DC.	Eremophysa	16	68	2	Jerusalem, Israel	Deserts
*A. kurdaicus Saposh.	Cystium	32	60	61	Taschkent, U.S.S.R.	Stony slopes of hills and mountains
*A. lagurus Willd.	Hymenostegis	32	31	34	Baku, U.S.S.R.	Dry stony mountain slopes at 1400-2400 m.
*A. lanuginosus Kar. et Kir.	Erionotus	16	69	69	Taschkent, U.S.S.R.	Plains, foothills, mountains, half-desert and desert regions
*A. lasiosemius Boiss.	Aegacantha	16	53	55	Taschkent, U.S.S.R.	With xerophytic vegetation at heights of 2300-3400 m.
A. leontinus Wulfen	Onobrychium	32	43	46	Neuchatel, Switzerland	Calcareous mountain slopes at 1000-2600 m.
A. leucacanthus Boiss.	Chronopus	16	1	11	Cairo, Egypt	Deserts
*A. longipetiolatus M. Pop.	Ammodendron	16	25	28	Ashkhabad #550, U.S.S.R.	Sandy places
A. macronyx Bge.	Myobroma	16	51	54	Taschkent, U.S.S.R.	Subalpine slopes with ephemerid vegetation
*A. macropelmatus Bge.	Myobroma	16	12	4	Rech. 10450, Iraq	
*A. macrourus Fisch. et Mey	Malacothryx	32	34	37	Baku, U.S.S.R.	Dry stony mountain slopes

TABLE I (cont'd)

Species	Section	2n	Fig.	Map	Seed Source	Habitat
*A. maximowiszii Trautv.	Eremophysa	16	23	25	Ashkhabad #511, U.S.S.R.	Sandy places
A. mongholicus Bunge	Cenanthrum	16	37	40	Copenhagen, Denmark	Prairie slopes and lightly wooded areas
*A. mossulensis Bge.	Onobrychium	32	10	1	Rech. 9675, Iraq Rech. 12720, Iraq	
*A. nigrimontanus M. Pop.	Chaetodon	32	52	53	Taschkent, U.S.S.R.	Stony light soils in plains and on mountain slopes with wormwood vegetation
*A. palmyrensis Post	Platyglottis	16	7	3	Rech. 9857, Iraq	Sandy soil and deserts
*A. penduliflorus Lam. =A. propinquus B.Schischk.	Cenanthrum	16	41	44	Brussels, Belgium	Dry places and rocky mountain slopes
*A. peregrinus Vahl.	Platyglottis	16	2	15	Cairo, Egypt	Sandy places and forest clearings
*A. peterfii Jav.	Calycocystis	64	29	32	Keszthely, Hungary	
*A. platyphyllus Kar. et Kir.	Proselius	16	46	52	Taschkent, U.S.S.R.	Prairie slopes in stony soils at 400-3000 m.
*A. platyraphis (Bge.)Fisch.	Myobroma	16	11	5	Rech. 12586, Iraq	Sandy places
*A. ponticus Pall.	Alopecias	64	35	38	Vacratot, Hungary	Prairies, mountain valleys, stony slopes and river banks

TABLE I (cont'd)

Species	Section	2n	Fig.	Map	Seed Source	Habitat
*A. purpureus Fom. =A. cyri Fom.	Proselius	16	38	41	Wroclaw, Poland	Sterile meadows and limestone slopes of mountains
A. richardsonii Sheldon	Hemiphragmium	48	44	74	Leningrad, U.S.S.R.	Tundra, on stony places
*A. römeri Simk.						
*A. sabulosus Jones	Preussii	26	91	89	University of Mighigan, U.S.A.	Barren clay slopes near rivers
*A. schelichovii Turcz.	Euodmus	16	26	29	Keszthely, Hungary	River valleys, sandy river banks, rarely in taija
A. scheremetevianus Fedtsch.	Scheremateviana	16	17	20	Leningrad, U.S.S.R.	Stony slopes of mountains to 3900 m., half-desert steppes
*A. schimperi Boiss.	Oxyglottis	16	14	19	Rech. 12826, Iraq	Sandy habitats
*A. schmalhausenii Bge.	Sewerzowia	16	24	27	Ashkhabad, U.S.S.R.	Woody foothills and low hills in light soil
*A. schrenkianus Kar et Kir.	Microcystis	16	50	51	Taschkent, U.S.S.R.	Sandy dry slopes of foothills
A. schugnanicus B. Fedtsch.	Brachycarpus	16	19	22	Leningrad, U.S.S.R.	Short grass meadows at 3000-3800 m.
A. sempervirens Lam.	Acanthophace	16	42	45	Neuchatel, Switzerland	Dry calcareous mountain slopes

TABLE I (cont'd)

Species	Section	2n	Fig.	Map	Seed Source	Habitat
A. sesamoides Boiss.	Oxyglottis	16	63	64	Taschkent #500, U.S.S.R.	South slopes of mountains, forest meadows, sandy river banks
**A. sieberi* DC.	Chronopus	16	5	13	Cairo, Egypt	Sandy places
A. skornjakovii B. Fedtsch.	Cystium	16	55	56	Taschkent, U.S.S.R.	Mountain slopes, high mountain prairies, semi-deserts
A. stenanthus Bge.	Hololeuce	16	47	49	Taschkent, U.S.S.R.	Mountain slopes in middle mountain areas
**A. suluklensis* Freyn. et Sint.	Malacothrys	48	30	33	Ashkhabad #556, U.S.S.R.	Prairie slopes of mountains
**A. terlinguensis* Cory	Micranthi	24	90	90	Univ. of Michigan, U.S.A.	Sandy or silty clay soils
**A. tibetanus* Benth.	Eu-Hypoglottis	16	48	48	Taschkent, U.S.S.R.	Mountain prairies, dense brush of foothills in middle and high level districts
**A. tribuloides* Del. var. *kirghisicus* (Schtschegleev) Sirj.	Oxyglottis	16			Rech. 9927, Iraq	Sandy soil, mountain plains, and steppe plains
A. tribuloides Del. var. *leiocarpus* Boiss.	Oxyglottis	16	13	7	Rech. 12545, Iraq	Sandy places and poor soils
**A. tugarinovii* N. Basil	Hemiphragmium	48	97	73	Leningrad, U.S.S.R.	Deciduous forests, bushy places, alpine tundra and river banks

TABLE I (cont'd)

Species	Section	2n	Fig.	Map	Seed Source	Habitat
*A. turkestanus Bge.	Christiana	16	59	60	Taschkent, U.S.S.R.	High foothill and middle hill districts
A. ugamicus M. Pop.	Xiphidium	82	65	66	Taschkent, U.S.S.R.	Light soils and rocky slopes of mountains
A. uninodus M. Pop. et Vved.	Harpilobus	16	61	62	Taschkent, U.S.S.R.	Terraces of river valleys, and slopes of low hills
*A. xanthomeloides E. Kor. et M. Pop.	Macrocystis	16	67	68	Taschkent, U.S.S.R.	Sandy or gravelly slopes of mountains
*A. xipholobus M. Pop.	Cytisodes	16	71	70	Taschkent, U.S.S.R.	Light soil in the foothill and lower mountain districts
Oxytropis						
O. arctica R.Br. ssp. taimyrensis Jurtz.	Orobia	64	75	78	Leningrad, U.S.S.R.	Dry places on stony or sandy rises
*O. argentea Pers.	Orobia	48	72	75	Helsinki, Finland	Prairies and open stony steppes of the foothills
O. chiliophylla Royle	Polyadena	16	83	86	Leningrad, U.S.S.R.	Stony slopes of mountains
O. foetida (Vill.)DC.		48	76	79	Udine, Italy	Dry grassy slopes of mountains, and rocky slopes
O. japonica Maxim.		16	78	81	Sapporo, Japan	
*O. karataviensis N. Pavl.	Physocarpon	16	81	84	Taschkent, U.S.S.R.	High stony slopes

TABLE I (cont'd)

Species	Section	2n	Fig.	Map	Seed Source	Habitat
*O. megalantha Boissieu	Orobia	32	84	87	Copenhagen, Denmark	
O. mertensiana Turcz.	Caeciabia	16	74	77	Leningrad, U.S.S.R.	Stony tundra
*O. nigrescens (Pall.) Fisch.	Arctobia	16	80	83	Leningrad, U.S.S.R.	Rocky slopes and rarely on sandy shores of rivers in Artic zone
O. schischkinii Vass.	Orobia	96	82	85	Leningrad, U.S.S.R.	In river valleys and on islands in rivers
*O. trichocalycina Bge.	Ptiloxytropis	16	79	82	Taschkent, U.S.S.R.	On upper mountain slopes in crushed stone
*O. uralensis Ldb.	Orobia	48	77	80	Linz-Oberdonau, Austria	Primarily on light, sandy soil on stony hillsides, prairie meadows, at forest edges

* Species for which there are voucher specimens or plants growing.

TABLE II

Chromosome counts for species of Astragalus for which there are previous published counts.

Species	Section	2n	Fig.	Map	Seed Source	Previous Counts
A. asper Wulf.	Pedina	48	95	96	Keszthely, Hungary	Tschechow (35) n = 24
*A. boeticus L.	Haematodes	30	86	92	Stanice, Czechoslovakia	Kreuter (29, 30) n = 8; Tschechow (35) 2n = 30; Ledingham (60) 2n = 30
*A. burkeanus Benth. = A. abyssinicus (Hochst.) Rich.	Diplotheca	16	88	99	Pretoria, South Africa	Ledingham (60) 2n = 16
o*A. campylorrhynchus Fisch. et Mey	Harpilobus	16	27	30	Ashkhabad #544, U.S.S.R.	Tschechow (35) n = 18
°A. campylotrichus Bge.	Campylotrichon	16	92	10	Taschkent #479, U.S.S.R.	Tschechow (35) n = 16
*A. chlorostachys Lindl.	Hymenostegis	16		16	Lucknow, India	Ledingham (60) 2n = 16
A. exscapus L.	Myobroma	16	94	98	Neuchatel, Switzerland	Tschechow (30) 2n = 16; Ledingham (60) 2n = 16
*A. litvinovii Lipsky	Dolicantha	16		71	Ashkhabad, U.S.S.R.	Ledingham (60) 2n = 16
*A. membranaceous (Fisch.) Bge.	Cenanthrum	16	93	95	Vladivostok, U.S.S.R.	Tschechow (30) 2n = 16
*A. mucronatus DC. = A. cicer L.	Eu-Hypoglottis	64	16	9	Rech. 15043, Armenia	Tschechow (35) 2n = 64

TABLE II (cont'd)

Species	Section	2n	Fig.	Map	Seed Source	Previous Counts
*A. pentaglottis L.	Trimeniaeus	28	85	93	Lisbon, Portugal	Senn (38) n = 14 Ledingham (60) 2n = 28
*A. schahrudensis Bge.	Alopecias	16	22	94	Ashkhabad, U.S.S.R.	Tischler (38) n = 8
*A. sinicus L.	Lotidium	16	96	97	Kobe, Japan	Kawakami (30) n = 8 Suqiura (31) 2n = 16
*A. somalensis Taub. ex Harms		20	87	91	K51102, Kitale, Kenya, East Africa	Ledingham (60) 2n = 20
*A. verus Oliv.	Platonychium	64	40	43	Amsterdam, Holland	Tschechow (35) 2n = 64
°*Oxytropis sulphurea (Fisch.) Ldb.	Orobia	16	73	76	Amsterdam, Holland	Ledingham (60) 2n = 48

° Counts which differ from previous published counts

* Species for which there are voucher specimens or plants growing.

DISCUSSION

Phylogenetic studies, although often grounded on established facts, contain a large degree of speculation.

> Ingenious men will readily advance plausible arguments to support whatever theory they shall choose to maintain; but then the misfortune is, everyone's hypothesis is each as good as another's since they are all founded on conjecture.
>
> Gilbert White, Selbourne; in a letter to Thomas Pennant, Esq., 29 May, 1769.

With this thought in mind, an attempt will be made to present some of the phylogenetic possibilities for Astragalus, with the full realization that the author does not have the comprehensive knowledge of this genus necessary for a complete interpretation, to say nothing of an understanding of the geology and the geography of the past which played such an important role in the evolution of the Angiosperms.

Astragalus is in the tribe Galegeae, subfamily Papilionoideae, of the family Leguminosae. This family is particularly interesting because of the great diversity of forms exhibited by its members. Trees, shrubs, and herbs are all found within the family. Astragalus species vary greatly, ranging from spiny perennial shrubs to short-lived annuals.

The evolution of the Angiosperms is now thought to have occurred in the late Jurassic. It was nevertheless during the Cretaceous that proliferation of this great group of flowering plants took place.

There has been much speculation and considerable conflict of opinion about the origin of the Leguminosae. The tropics seem to be the most likely home of this family. The idea of a tropical origin was first suggested in 1855 by Alphonse de Candolle. Evidence that has been gathered since that time supports this belief. In 1936, Szymkiewicz published data which showed the greatest concentration of legume genera in the tropics. Brazil led the list with 130 genera. The Indies were next with 98, followed closely by South Africa with 97 and the Congo with 92.

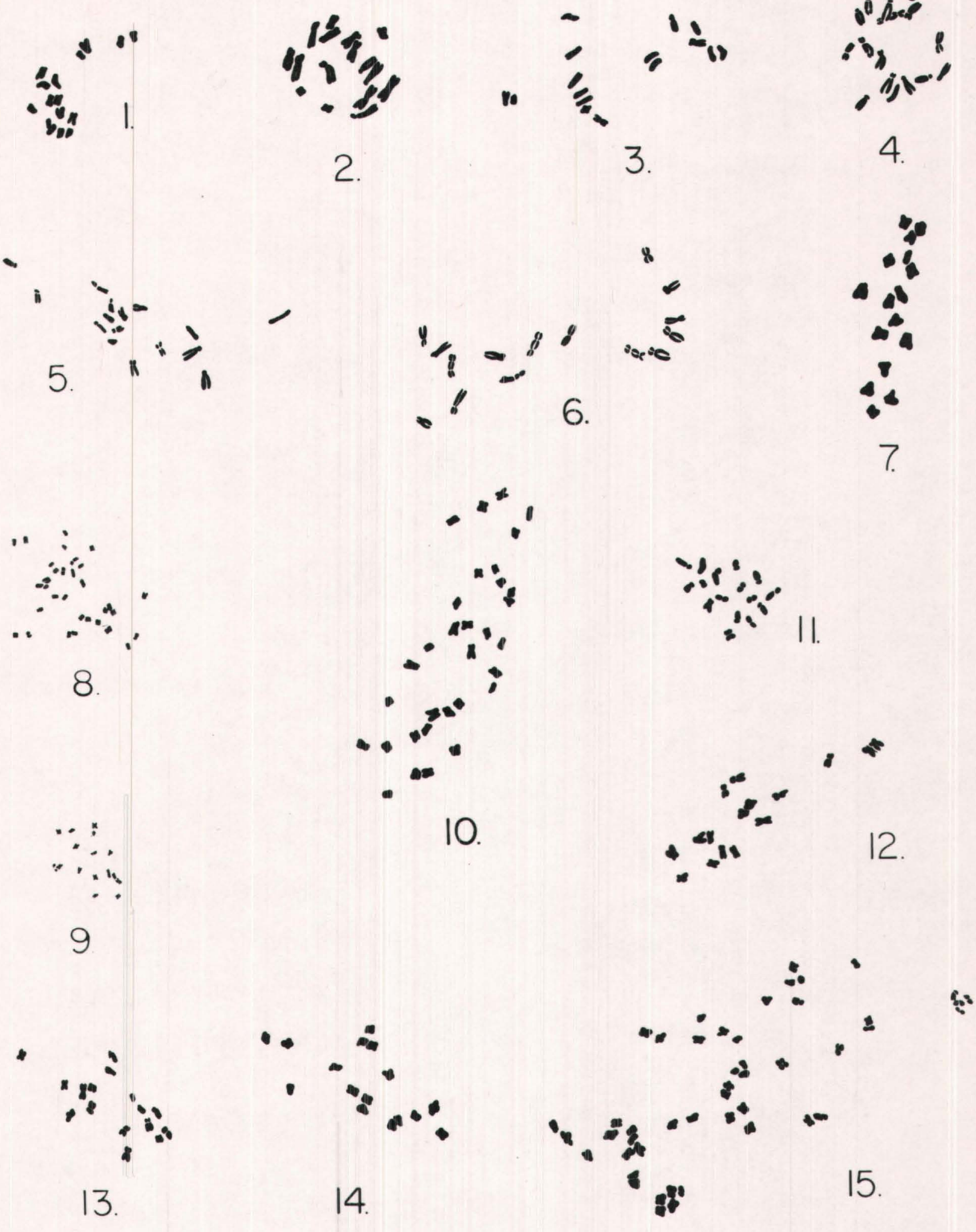
The derivation of the Leguminosae was probably from some primitive, primary form which is no longer in existence. The exact nature of this primitive ancestor can only be guessed at,however, Andrews (1914) presented the following as a likely form:

> Postulated ancestral forms were trees, shrubs, undershrubs, and climbers of luxuriant habit. Leaves alternate, stipulate, mainly simple, in some cases digitate or trifoliate, more rarely simply pinnate and possessing more than three leaflets. Corolla regular, the petals overlapping, petals five, rarely four. Stamens free, as many or twice as many as petals, rarely indefinite. Style of one carpel, the ventral suture always directed to the dorsal aspect of the flower. Carpel unilocular and bearing ovules in either one or two rows on the ventral suture. Fruit a pod or drupe. Seeds rarely albuminous.

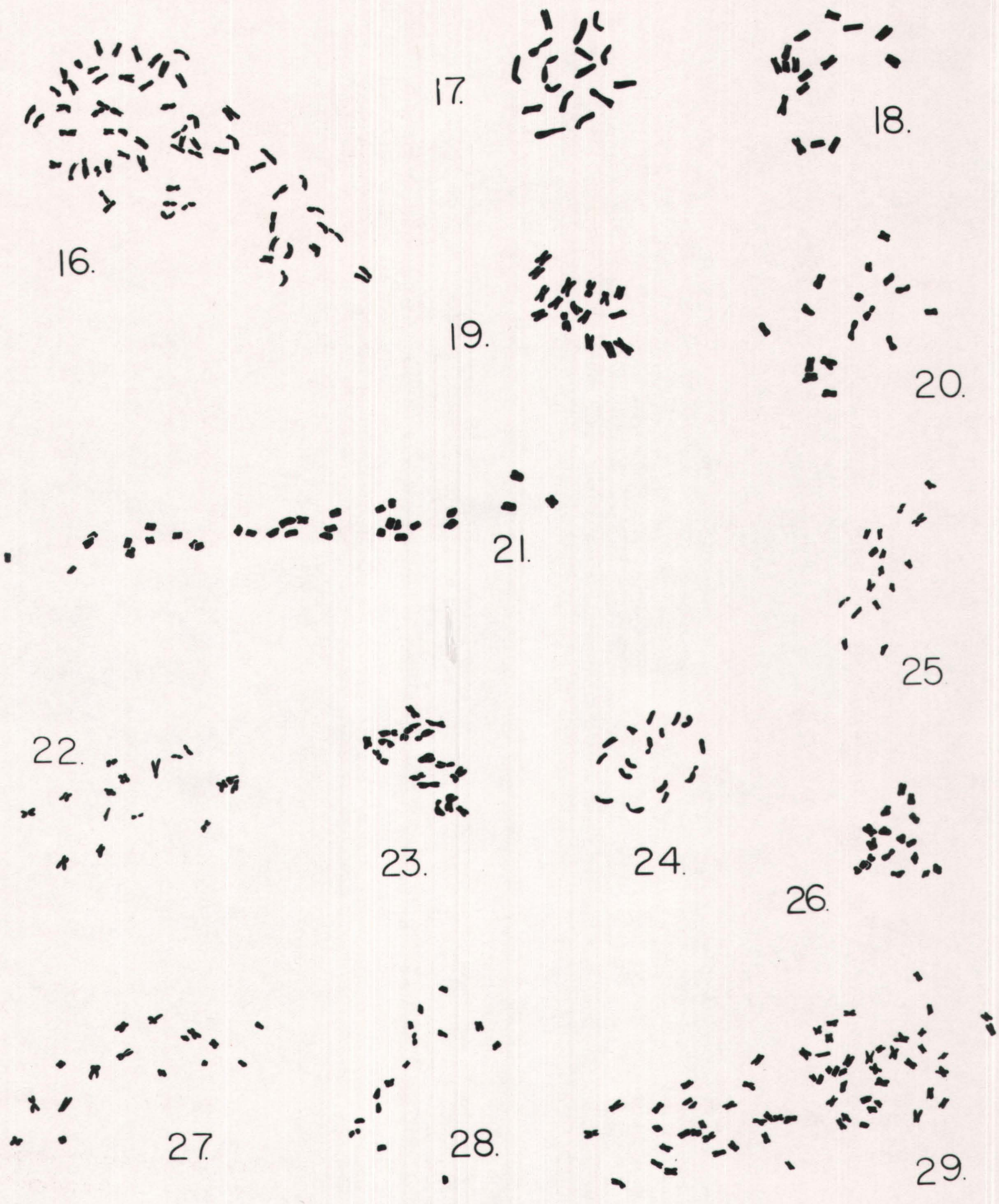
The family Leguminosae is divided into three subfamilies: Mimosoideae, Caesalpinioideae, and Papilionoideae. The first two subfamilies mentioned are recognized as being characteristic of tropical regions. The Papilionoideae, however, are found primarily in subtropical climates rather than tropical environments. The members of this last subfamily, which includes the genus Astragalus, extend to the limits of dicot vegetation in both the northern and southern hemispheres.

It is evident that the Papilionoideae are highly modified plant types, and that free stamens and regular corollas characterized the more primitive types of the order.

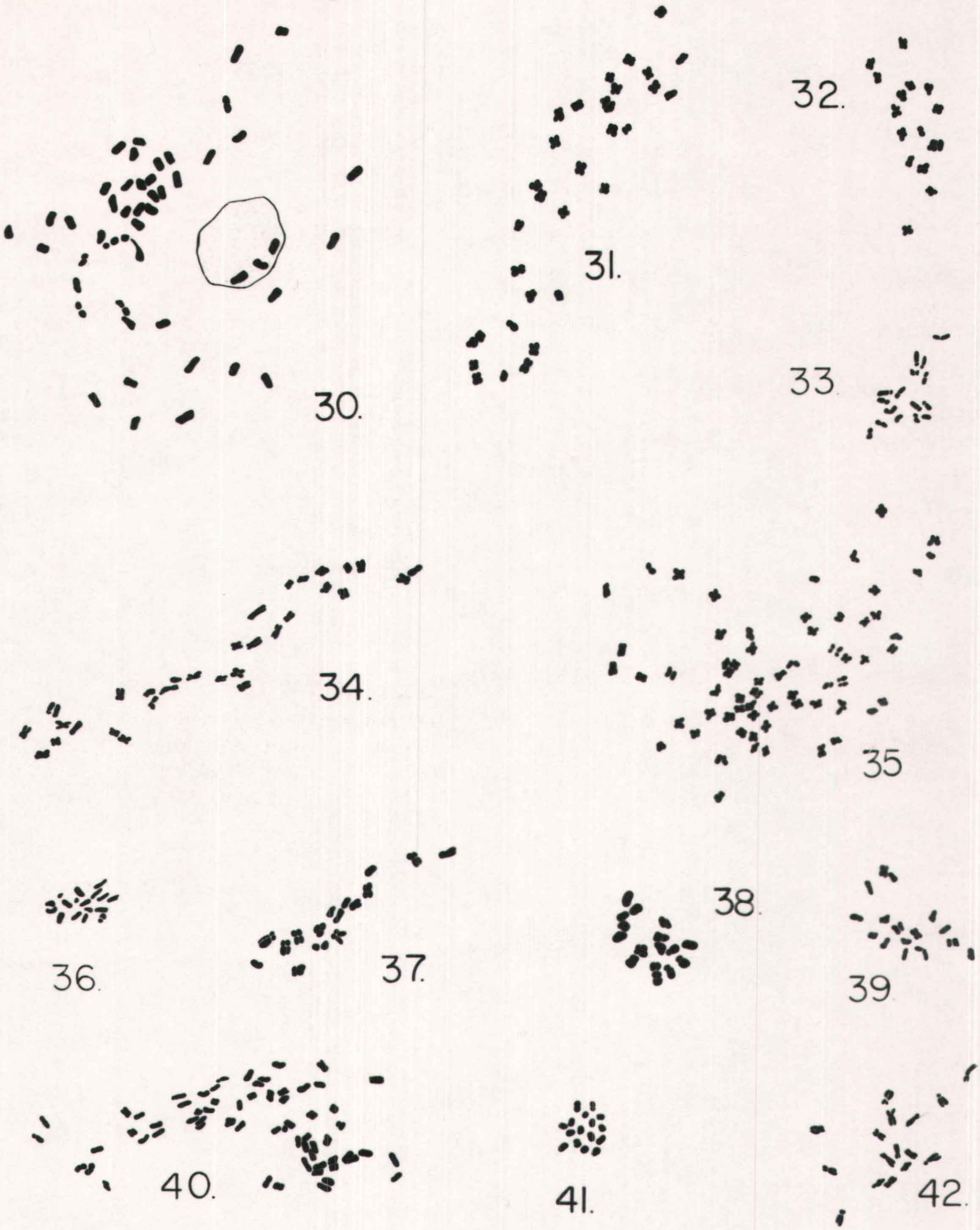
Although many genera of this subfamily are tropical, the majority, including Astragalus, appear to have developed in dry barren lands after differentiation of the family was well underway.



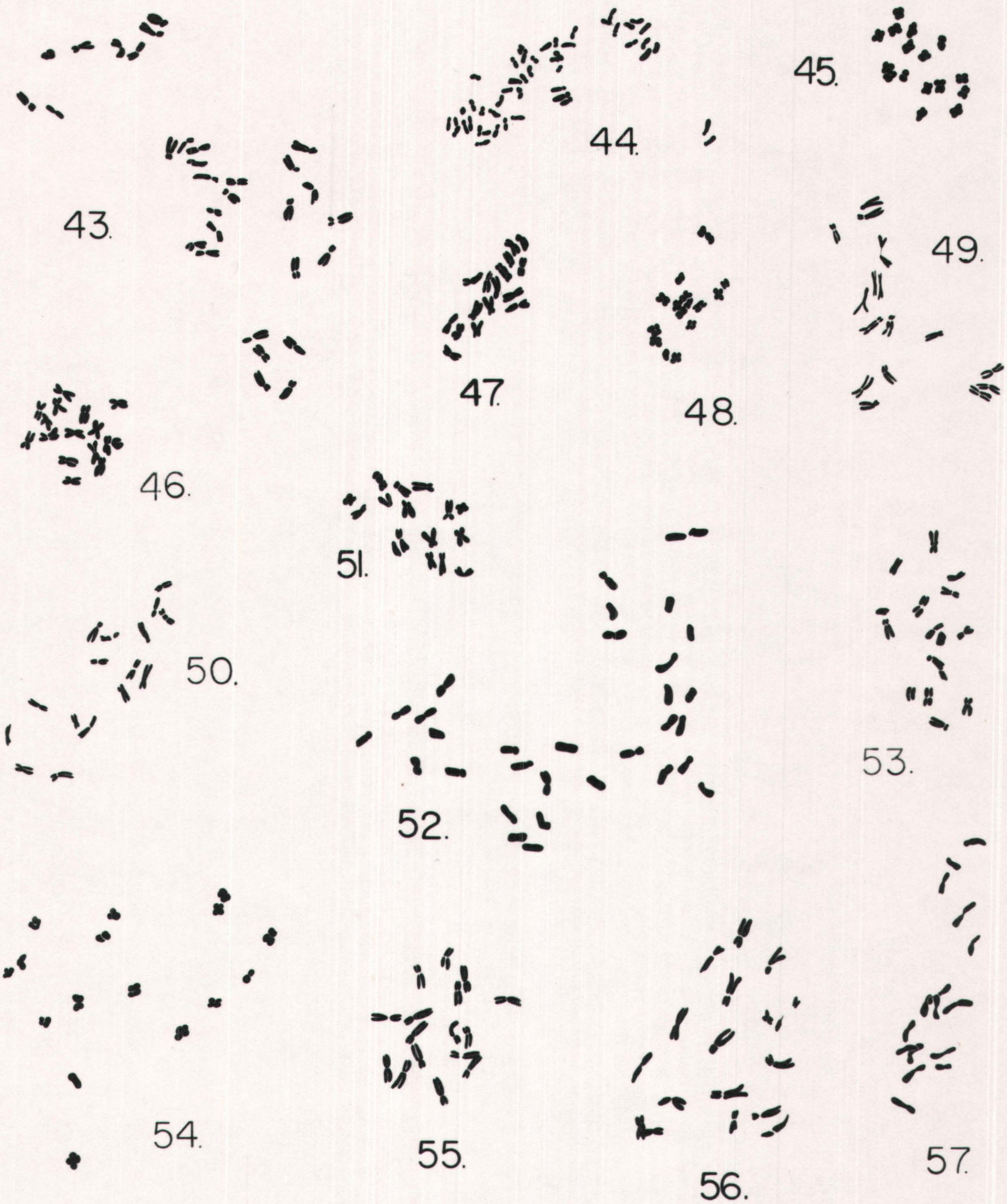
FIGURES 1-15: 1. *A. leucacanthus* Boiss. (2n=16); 2. *A. peregrinus* Vahl. (2n=16); 3. *A. hispidulus* DC. (2n=16); 4. *A. bombycinus* Boiss. (2n=16); 5. *A. sieberi* DC. (2n=16); 6. *A. alexandrinus* Boiss. (2n=16); 7. *A. palmyrensis* Post (2n=16); 8. *A. corrugatus* Bert. (2n=32); 9. *A. finitimus* Bge. (2n=16) x765; 10. *A. mossulensis* Bge. (2n=32); 11. *A. platyrahphis* Fisch. (2n=16); 12. *A. macropelmatus* Bge. (2n=16); 13. *A. tribuloides* Del. var. *leiocarpus* Boiss. (2n=16); 14. *A. schimperi* Boiss. (2n=16); 15. *A. gyzensis* DC. (2n=48). Camera lucida drawings x1530 except where stated otherwise.



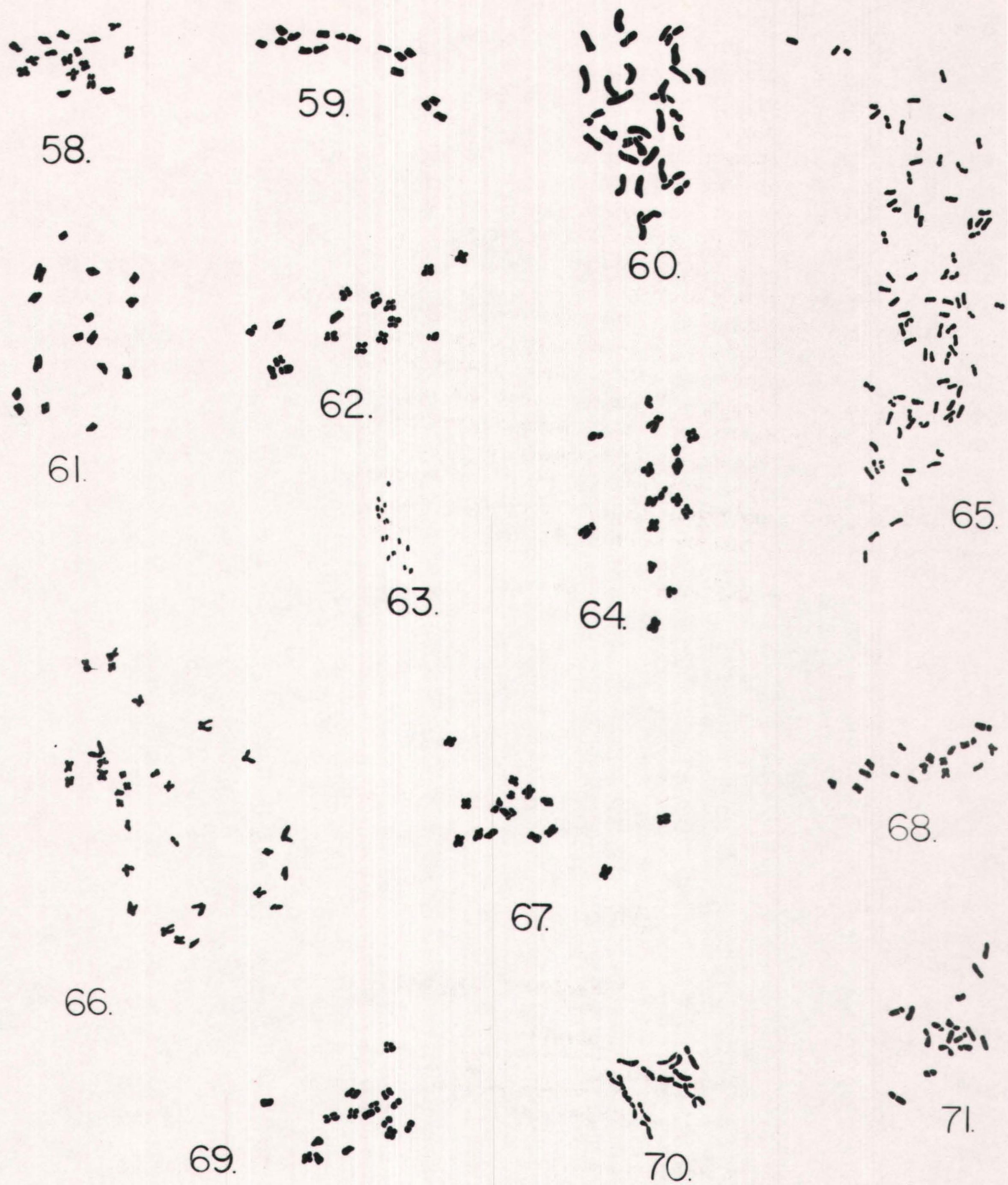
FIGURES 16-29: 16. *A. mucronatus* DC. (2n=64); 17. *A. scheremetevianus* B.Fedtsch. (2n=16); 18. *A. heterodontus* Boriss. (2n=16); 19. *A. schugnanicus* B.Fedtsch. (2n=16); 20. *A. brachypetalus* Trautv. (2n=16); 21. *A ackerbergensis* Freyn (2n=32); 22. *A. schahrudensis* Bge. (2n=16); 23. *A. maximowiszii* Trautv. (2n=16); 24. *A. schmalhausenii* Bge. (2n=16); 25. *A. longipetiolatus* M. Pop. (2n=16); 26. *A. schelichovii* Turcz. (2n=16); 27. *A. campylorrhynchus* Fisch. et Mey. (2n=16); 28 *A. interpositus* Boriss. (2n=16); 29. *A. peterfii* Jav. (2n=64). Magnification 1530x.



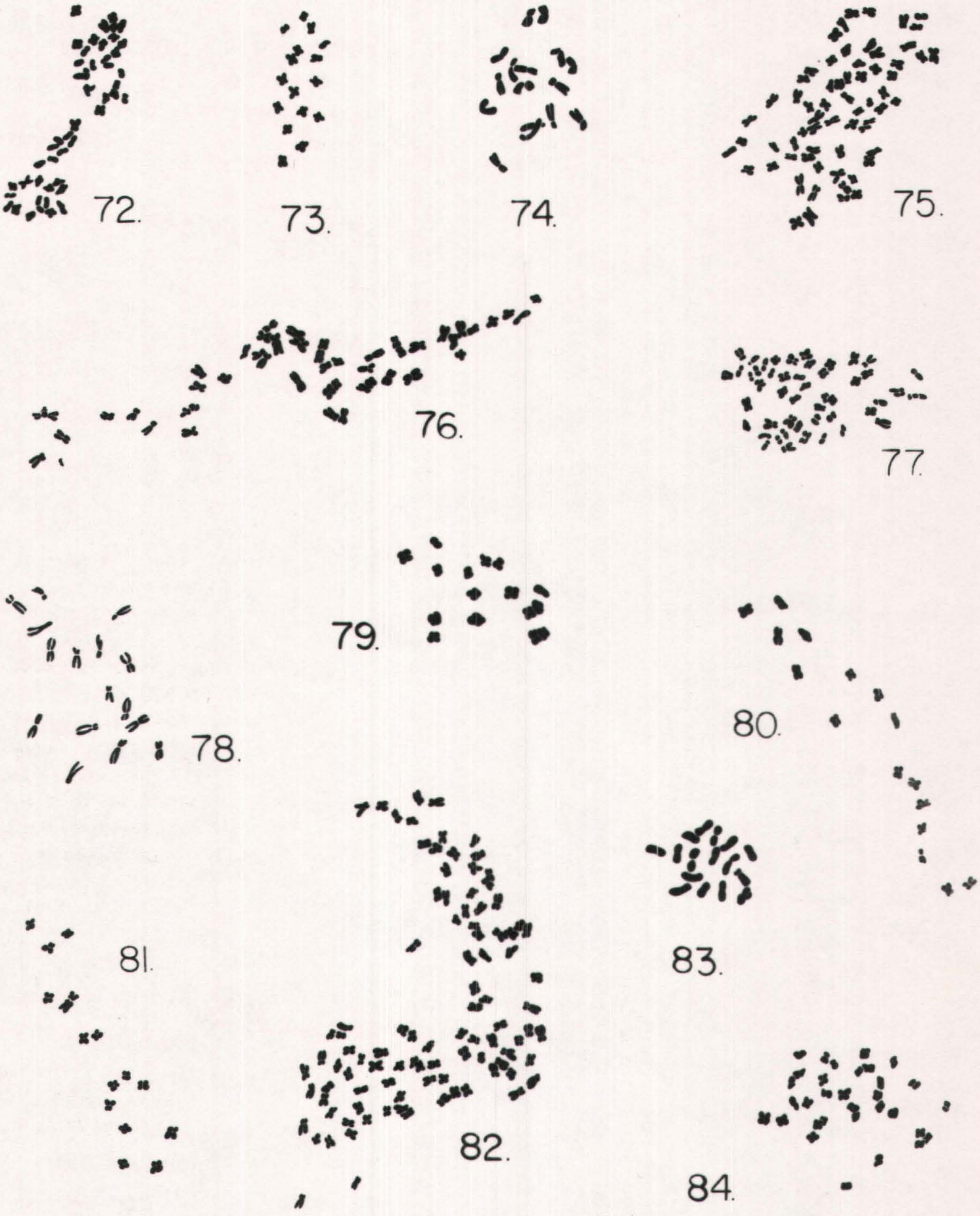
FIGURES 30-42 : 30. *A. suluklensis* Freyn et Sint. (2n = 48); 31. *A. lagurus* Willd. (2n = 32); 32. *A. andreji* Rzazade (2n = 16); 33. *A. aksuense* Bge. (2n = 16); 34. *A. macrourus* Fisch. et Mey. (2n = 32); 35. *A. ponticus* Pall. (2n = 64); 36. *A. expansus* Boiss. (2n = 16); 37. *A. mongholicus* Bunge (2n = 16); 38. *A. purpureus* Fom. (2n = 16); 39. *A. illyricus* Bernh. (2n = 16); 40. *A. verus* Oliv. (2n = 64); 41. *A. penduliflorus* Lam. (2n = 16); 42. *A. sempervirens* Lam. (2n = 16). Magnification 1530x.



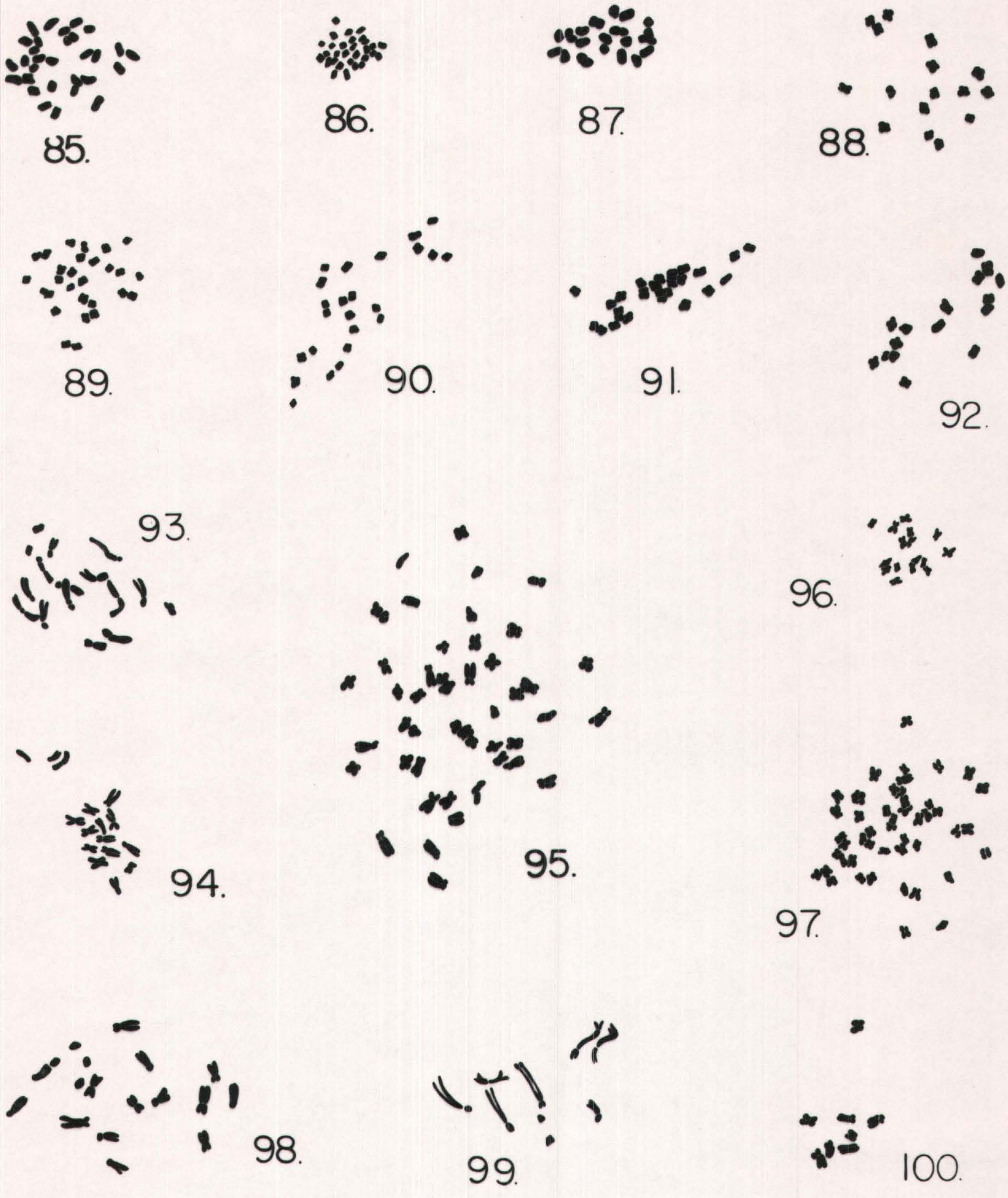
FIGURES 43-57: 43. *A. leontinus* Wulfen (2n=32); 44. *A. richardsonii* Sheldon (2n=48); 45. *A. coluteocarpus* Boiss. (2n=16); 46. *A. platyphyllus* Kar. et Kir. (2n=16); 47. *A. stenanthus* Bge. (2n=16); 48. *A. tibetanus* Benth. (2n=16); 49. *A. eremospartoides* Rgl. (2n=16); 50. *A. schrenkianus* Kar. et Kir. (2n=16); 51. *A. macronyx* Bge. (2n=16); 52. *A. nigrimontanus* M. Pop. (2n=32); 53. *A. lasiosemius* Boiss (2n=16); 54. *A. alopecias* Pall. (2n=16); 55. *A. skornjakovii* B. Fedtsch. (2n=16); 56. *A. hissaricus* Lipsky (2n=16); 57. *A. eximius* Bge. (2n=16): Magnification 1530 x.



FIGURES 58 - 71: 58. *A. iskanderi* Lipsky (2n=16); 59. *A. turkestanus* Bge. (2n=16); 60. *A. kurdaicus* Saposh. (2n=32); 61. *A. uninodus* M. Pop. et Vved. (2n=16); 62. *A. cottenianus* Aitch et Baker (2n=16); 63. *A. sesamoides* Boiss (2n=16), 765x; 64. *A. globiceps* Bge. (2n=16); 65. *A. ugamicus* M. Pop. (2n=82), 765x; 66. *A. bungei* C. Winkl. et Fedtsch. (2n=32); 67. *A. xanthomeloides* Eug. Kor. et M. Pop. (2n=16); 68. *A. kahiricus* DC. (2n=16); 69. *A. lanuginosus* Kar. et Kir. (2n=16); 70. *A. amalecitanus* Boiss (2n=16); 71. *A. xiphilobus* M. Pop. (2n=16). Magnification 1530 x except where otherwise specified.



FIGURES 72-84: 72. *O. argentea* Pers. (2n=48); 73. *O. sulphurea* Fisch. (2n=16); 74. *O. mertensiana* Turcz. (2n=16); 75. *O. arctica* R. Br. ssp. *taimyrensis* Jurtz. (2n=64); 76. *O. foetida* (Vill.) DC. (2n=48); 77. *O. uralensis* Ldb. (2n=48); 78. *O. japonica* Maxim. (2n=16); 79. *O. trichocalycina* Bge. (2n=16); 80. *O. nigrescens* (Pall.) Fisch. (2n=16); 81. *O. karataviensis* N. Pavl. (2n=16); 82. *O. schischkinii* Vass. (2n=96); 83. *O. chiliophylla* Royle (2n=16); 84. *O. megalantha* Boissieu (2n=32). Magnification 1530x.



FIGURES 85 - 100: 85. *A. pentaglottis* L. (2n = 28); 86. *A. boeticus* L. (2n = 30); 87. *A. somalensis* Taub. ex Harms (2n = 20); 88. *A. burkeanus* Benth. (2n=16); 89. *A. hypoleucus* Schauer (2n = 28); 90. *A. terlinguensis* Cory (2n = 24); 91. *A. sabulosus* Jones (2n = 26); 92. *A. campylotrichus* Bge. (2n = 16); 93. *A. membranaceus* (Fisch.) Bge. (2n = 16); 94. *A. exscapus* L. (2n = 16); 95. *A. asper* Wulf. (2n = 48); 96. *A. sinicus* L. (2n = 16); 97. *A. tugarinovii* N. Basil (2n = 48); 98. *A. mongholicus* Bunge (2n = 16); 99. *A. mongholicus* Bunge (n = 8); 100. *A. mongholicus* Bunge (n = 8). Magnification 1530 x.

Many problems in the phylogeny and distribution of plants and animals involve the interpretation of the occurrence of the same or related forms in both the Old World and the New World. The solution to many of these problems in the distribution of flora and fauna hinges on whether or not the continents have changed position relative to one another during preceding periods of geological time. Did the phenomenon of continental drift actually occur? Were there land bridges connecting continents which are now separated by thousands of miles of ocean? The answer to these problems would provide the key to biogeography on a world-wide scale.

Many people, such as Wulff, 1950, accept the fact that a land bridge once connected Alaska and eastern Siberia. Similarily, a connection of some form between Africa and South America is often postulated, and indeed, accepted as a fact by many biogeographers (Croizat, 1958). Many discontinuous distributions of both plants and animals could be explained without trouble by this theory. This latter connection, if it did exist, was broken before the great upheavals that marked the mountain building of the Tertiary. A recession of oceans, formation of deserts, and separation of land masses accompanied these disturbances in the earth's crust.

F. B. Taylor in 1908 published the first convincing presentation of the Theory of Continental Drift. However, it was the presentation of A. Wegener in 1912 which challenged current opinions and opened up a worldwide controversy on the subject. In the maps presented by Köppen and Wegener, 1924, a wide connection was shown to have existed between South Africa and South America in the Jurassic after the separation of the continents had begun. A northern connection between northwestern

Europe and northeastern North America was thought to have persisted up to the Cretaceous. By the Cretaceous a narrow stretch of water separated the two southern continents.

It is quite possible that the primitive ancestor of the Leguminosae could have become widespread across the tropics during the late Cretaceous when the climate was generally warm and moist. With the upheavals of the mountains and the subsequent resulting areas of severe climate where rigorous growth conditions prevailed, xerophytic forms evolved or at least underwent a great expansion. It is quite possible that xerophytic forms had evolved prior to the mountain building era. They were likely restricted to limited areas where barren, sandy soils presented more exacting conditions than those found generally at the time. A gradual contraction of areas where food and moisture were readily available fostered the rapid development and diversification of xerophytic forms.

As can be seen by the general distribution of the genus (Map 100), there are three areas of primary concentration for Astragalus. Central and southwestern Asia, western North America and western South America. The largest number of species is found in the Eurasian region. Komarov (1946) lists 849 species of Astragalus and 276 species of Oxytropis in his Flora of the U.S.S.R.

Oxytropis, with just over 300 species, has a predominantly north temperate distribution (Map 101). The largest number of species is found in Central Asia. The genus is represented by a few additional species in Northern and Central Europe. A small number of species are found in Asia Minor, but none are known from Africa or the Sinai area. In the New World, the genus is restricted to North America where only 22 species are recognized. The members of the genus are most abundant in the North, however, one species extends as far south as Texas and three to California.

The immense Eurasian land block appears to be the home of many of the important legume genera. Andrews (1914) gives this area as the place of origin of both _Astragalus_ and _Oxytropis_ as well as _Adenocarpus_, _Ulex_, _Cystius_, _Ononis_, _Genista_, _Trigonella_, _Medicago_, _Melilotus_, _Trifolium_, _Caragana_, _Hedysarum_, _Onobrychis_, _Vicia_, _Lathyrus_, _Pisum_, and many others. The Central Asian origin of _Astragalus_ and _Oxytropis_ seems to be assumed by most authors. This conclusion has been based largely on the fact of the great proliferation of species in this region, and the fact that this central region was relatively stable with regard to continental shifts, extension of seas and so forth. The postulated extension of the range of _Astragalus_ is from the Mediterranean and Eurasian steppes to North America across the Siberian Bridge and thence along the Cordillera to the Andes of Chile and Argentina. The absence of the genus in Australia is explained by its failure to cross the tropics to Australia from its extratropical place of origin because of the lack of plateaus needed to bridge the areas with unfavorable growth conditions existing in the Indo-Malayan Region.

The habitats in which _Astragalus_ species are known to exist are characterized by lacking most of the conditions considered advantageous to plant growth. Most of the species are found in poor soils. Desert sands and gravelly places are popular. Arid conditions are preferred. Although many species are found on mountain slopes or steppes, just as many are found in barren half-deserts or deserts.

It is interesting to note that a few species include wooded areas or forests in their range of habitats. This fact could provide a clue to the sequence of habit changes in the evolution of the genus. It is plausible to suggest that the ancestors from the tropical forest first adapted to the drier, but still relatively lush conditions of the temperate forest, then to the more exacting conditions of the dry grasslands and desert sands.

On the other hand, an adaptation from poor conditions to the more moist forest habitats could have occurred. This adaptation, if it did occur, would be a more recent one. The answer to this habitat problem might be obtained if a comprehensive study were made of the past and present climatic and geological conditions along the supposed migration routes of Astragalus and Oxytropis.

Speciation in such a large genus as Astragalus cannot be explained entirely by geographic factors. In a large number of papilionaceous species, cleistogamous flowers are characteristic. Atchison (1951) suggested that in the Papilionoideae, the isolating effect of cleistogamy could be equal to that of geography. Among the species of Astragalus which have reached the flowering stage in the garden or greenhouse in Regina, only three species, two Old World and one New World, have had cleistogamous flowers. A. hamosus L. and A. boeticus L. were the Old World species, and A. lotiflorus Hook. was the New World species. There appear to be a large number of self-pollinated annuals in the genus. The following species have set fruit almost as soon as the flowers opened without the aid of insects or tripping: A. sesamoides Boiss., A. rytilobus Bge., A. uninodus M. Pop. & Vved., A. bungei C. Winkl. & Fedtsch., A. palmyrensis Post, A. cruciatus Link., A. bombycinus Boiss., A. tribuloides Del., A. schimperi Boiss., A. gyzensis DC., A. corrugatus

Bert., *A. hispidulus* DC., and *A. pentaglottis* L.

The method by which speciation can occur in the grass family as outlined by Stebbins (1950) could be similar in the self-pollinated species of *Astragalus*. The term biotype will be used in the following discussion to mean all of the individuals with the same genotype. A self-pollinated race which can maintain itself for many generations can become completely homozygous. If a chance hybridization occurs between two biotypes, the resulting offspring will be highly heterozygous. Extensive segregation of the progeny of the F_1 (six to eight generations) would result in many new genotypes, some of which would likely be better adapted to ecological conditions than the parent biotypes. The races which survived segregation and selection could then stabilize through inbreeding and form new biotypes. Thus speciation would be the result of short bursts of evolution.

Polyploidy has played some part in speciation in *Astragalus* and *Oxytropis*. Of the species counted in these two genera, 17.4% are polyploids. *Oxytropis* has the higher rate of polyploidy with 25.8% while *Astragalus* has only 16.3%. The occurrance of polyploidy appears to be independent of geographic distribution in the Old World. Of the presently known species numbers in the New World, only one, *Astragalus grayi* Parry, has a polyploid number. An extensive crossing program in *Astragalus* and *Oxytropis* could produce useful information about the genetic systems of these genera.

Theories on the distribution of *Astragalus* have been based on the idea of a single origin of the genus. Until recently, the different chromosome numbers of the New World and Old World species were not generally known. Senn (1938) did not list any counts of *Astragalus* species with n = 11, 12, or 13. Ledingham's paper in 1960 gave a clear idea of the split in basic number between the two geographic areas, based on a list of chromosome counts which had been greatly extended since Senn's paper was published. This distinct split in base numbers, with n = 8 in the Old World and n = 11, 12, or 13 in the New World, gave rise to the idea of two separate genera, possibly with separate origins.

With such a large genus as Astragalus it has been possible to take only a small number of the total of approximately 2000 species on which to make further chromosome counts and on which to base any conclusions regarding the phylogeny of the genus. As previously stated, the species for counting were selected at random. The results of the sampling may be regarded as something of a Gallup Poll which carries no guarantee of infallibility.

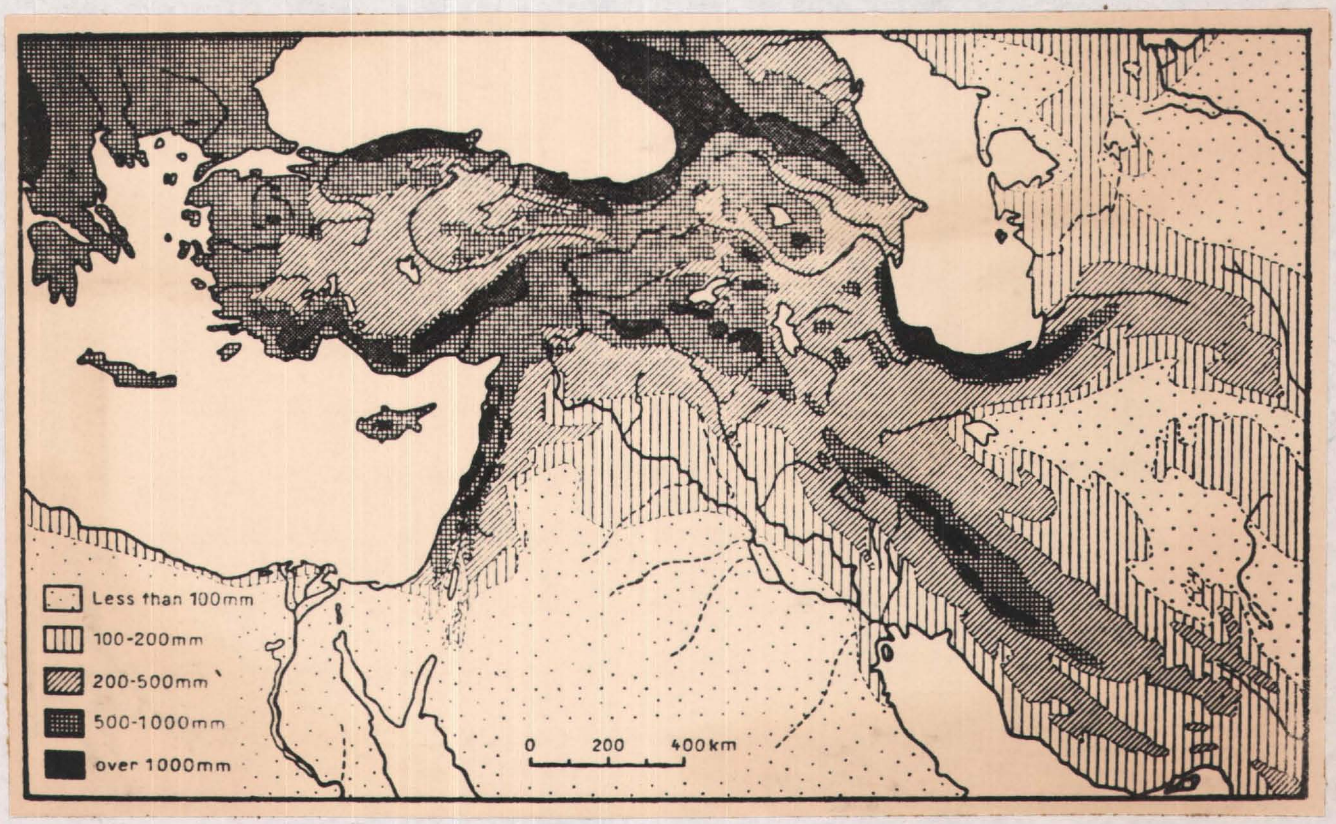
A count of 2n = 20 for A. somalensis Taub. ex Harms was reported by Ledingham (1960). This species is reported only from southern Ethiopia. It was thought that an intermediate series might exist between the n = 8 numbers of the Old World and the n = 11, 12 or 13's of the New World. If any 9's or further 10's were to be found, it would be likely that they would be found in the same geographical area as A. somalensis. Unfortunately, there are very few species of Astragalus in Africa except in the north in the countries that border the Mediterranean. The other species known are A. galega (2n = 32), A. venosus (Hochst.) A. Rich. (2n = 16), and A. abyssinicus (Hochst.) Rich. (2n = 16). Changes in the climatic conditions since the Tertiary account for the impoverishment of the vegetation of certain regions of Africa. This fact might explain the scarcity of Astragalus species especially in West Africa, The northern part of Africa from Morocco to Egypt has a considerable sampling of Astragalus. Members of the genus have a prominent place in the vegetation of the Atlas range, the coastal sands, and the oases of the deserts.

Wulff (1937) published an interesting paper in which he divided the world into phytogeographic regions according to the numerical distribution of species. He noted five apparent regularities in distribution:

1. An impoverishment of vegetation north and south of the equator due to temperature changes.
2. A smaller number of species in the subtropical desert and steppe zones north and south of the equator due to decrease in moisture.
3. A decrease in the number of species in Europe from west to east. This condition is likely due to a lack of moisture. The same situation is true in North Africa as you progress from the mountainous regions of Morocco and Algeria to the dry deserts of Egypt.
4. A numerical richness of species is peculiar to mountain massifs.
5. The numerical abundance of species is connected with the antiquity of the flora in that region.

Although these factors are true for the total vegetation of the earth, only the last two are true for the genus Astragalus. Because of the temperate nature of this genus, the greatest concentration of species is outside of the tropical regions. The number of species found in subtropical deserts and steppe zones is understandably high because so many members of the Astragalus group are xerophytes. The number of species in western Europe is smaller than the number of species in eastern Europe. This condition is related to an increase in the number of suitable habitats for the genus as you progress towards the Asian center of distribution.

In the north African region, Morocco and Algeria have approximately 2000 to 3000 species of plants. In Tunisia the number of species is less than 2000. In the region of the Sahara Desert the flora is further impoverished to include only about 300 species. An increase in the number of species to nearly 3000 in northeastern Africa is accounted for by the fact that this area includes the mountainous regions of Abyssinia. Astragalus again avoids the more favorable conditions. There are 37 species listed in Egypt (Täckholm, 1956). Although the floras of Morocco and Algeria were not available, the number of species is known to be less from references in other texts.



MAP A. Mean annual rainfall in the Near East. Designed: K. W. Butzer.

Geographic Area	No. of spp.	Gametophyte Chromosome Number													
		8	10	11	12	13	14	15	16	22	24	32	41	48	>48
Total	282	143	1	40	31	14	3	1	18	1	16	10	1	2	1
Old World	179	134	1				2	1	13		14	10	1	2	1
New World	103	9		40	31	14	1		5	1	2				
South America	9			2		7									
United States	59			29	24	5	1								
Canada and Alaska	35	9		9	7	2			5	1	2				

FIGURE 101. The relation between chromosome number and geographic area in *Astragalus* and *Oxytropis*.

Many of the Astragalus species found in North Africa can be shown to be of either European or Asian origin. The Asian species have spread quite recently to Africa through the Sinai gateway. The European species likely migrated from the Iberian peninsula to Morocco by way of a Tertiary land connection between these two regions. Almost all of the species counted from North Africa have a base number of 8. The two certain exceptions are A. pentaglottis L. with 2n = 28 and A. boeticus L. with 2n = 30. These are likely the result of aneuploid losses from the tetraploid 2n = 32. The report of Kreuter (29, 30) of n = 8 for A. boeticus L. is likely the result of a confusion with Phaca boetica L. which is now A. lusitanicus Lam. This species has 2n = 16. A report of n = 14 for A. edulis Dur. from Morocco was made by Kreuter in 1930. In his paper, he questioned this count strongly. Cells with n = 15 and n = 16 were reported for this species in his paper. It would seem to the author that the most likely number for A. edulis is n = 16. It is interesting to note that most of the aberrant counts to date in this genus are from the Mediterranean region. A further study of species from this area would be useful in determining whether or not the tendency toward a reduction in chromosome number is actually more common than is supposed at this time. The complete absence of 9's and the single 10 previously counted and confirmed here, would leave room for questioning whether or not A. somalensis has been correctly placed within the genus Astragalus.

It is very unlikely that Astragalus was widespread in Africa during the Cretaceous when the only possibility of migration between Africa and the New World could have existed. It is more likely that the genus did not evolve until the Upper Cretaceous and did not undergo

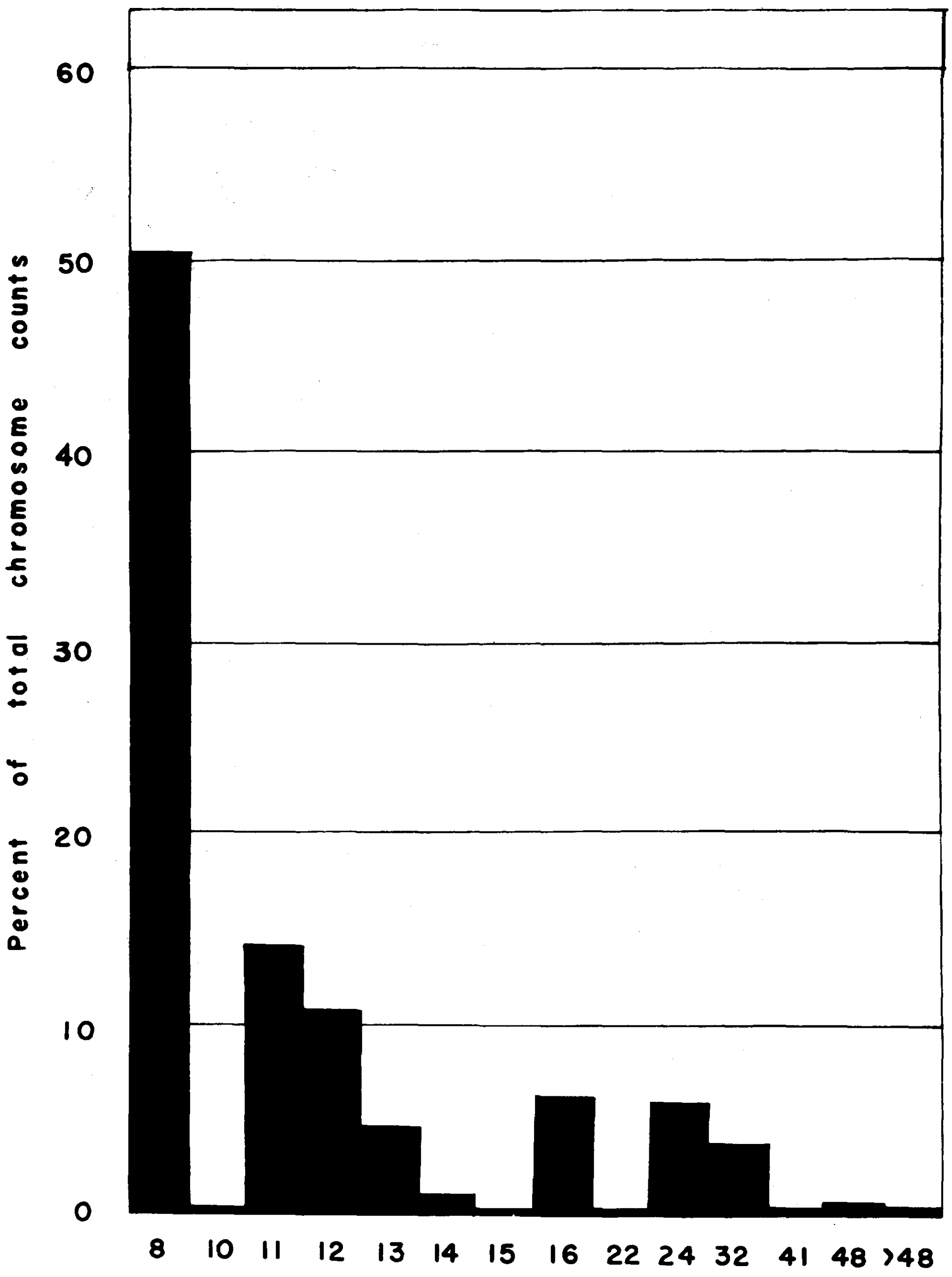


FIGURE 102. Percentage of gametophyte chromosome numbers in *Astragalus* and *Oxytropis*.

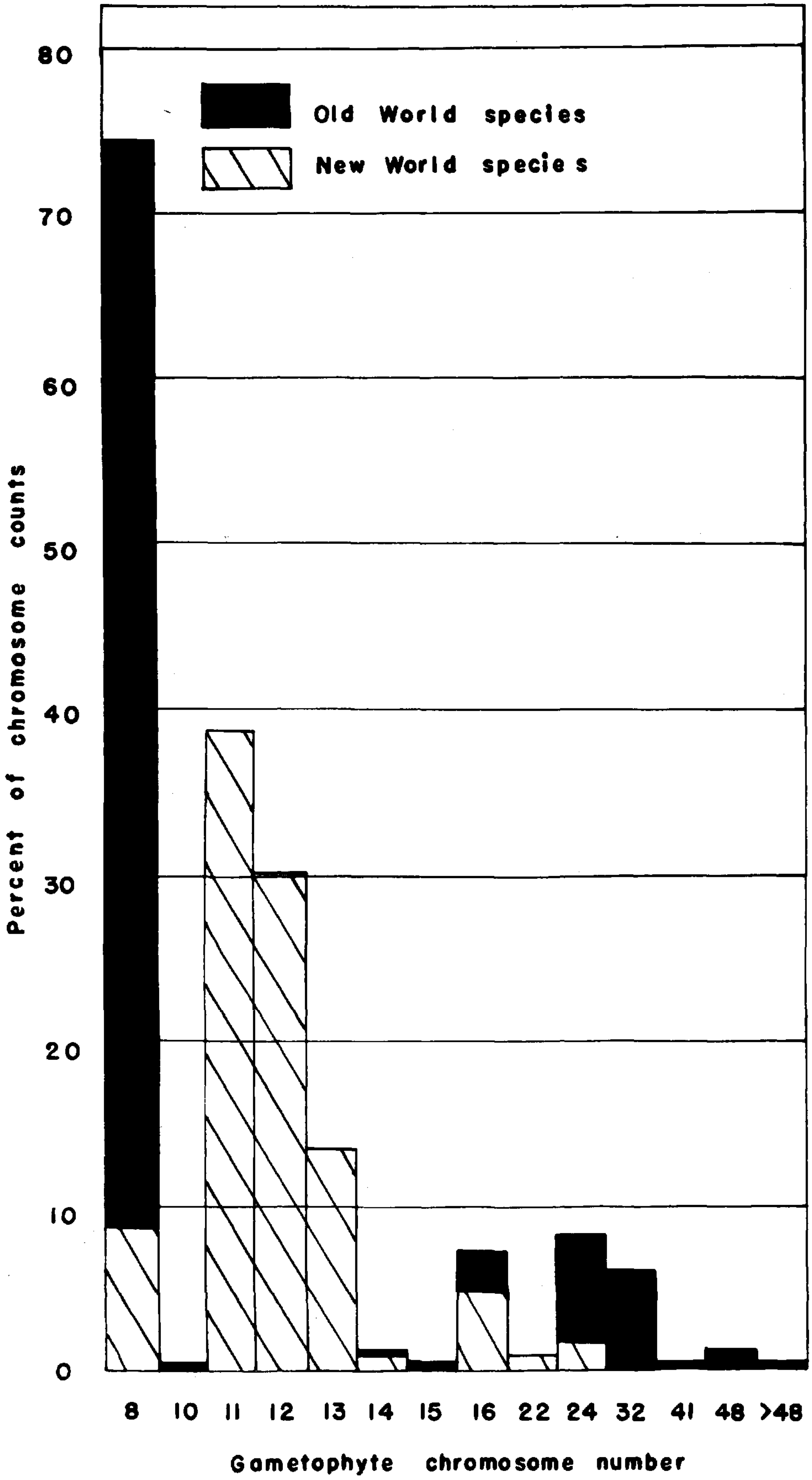


FIG. 103. Percentage of gametophyte chromosome numbers in Old World and New World species of *Astragalus* and *Oxytropis*.

full-scale expansion until the Tertiary. If this is true, the probability of an exchange between Africa and South America is very low. If, however, the dispersal time has been misjudged, the clues to the mystery of the ancient exchange have been lost in the Sahara's shifting sands. Perhaps South America holds the key to this mystery, but at present there seems to be no evidence to support the derivation of the New World Astragalus from the Old World Astragalus or vice versa.

At this point it is necessary to stress again the sharp differentiation in the chromosome numbers in the Old and New World species of Astragalus. Figure 101 summarizes the gametophyte chromosome counts known in the genus Astragalus up to the time of the submission of this thesis. The total number of Old World counts recorded is considerably more than the number of New World counts recorded. This partially accounts for the high percentage of $n = 8$'s in the total number of species counted (Figure 102). If, however, the graph (Figure 103) showing the percentages of gametophyte numbers in both Old and New World species individually is observed, the complete absence of the $n = 11, 12, 13$ group in the Old World and the dominance of this group in the New World is the most striking point illustrated. This graph gives a truer picture of the actual chromosome relationships.

One fact stands out above all others gathered from this study. The chromosome number in the genus Astragalus is definitely a constant character. Of the new counts made, all except one of the Old World species showed the basic number of 8. The Oxytropis species counted also had a base number of eight. This similar chromosome number confirms the taxonomists' opinion of the close relationship between Old World Astragalus and Oxytropis. The constancy of chromosome number would tend to confirm the value of this character in taxonomic studies, at least, in these genera.

The presence of species with the base number 8 in the New World accounted for by the crossing of these species, or close relatives, from Siberia to Alaska while these two areas were still connected. This crossing was followed by a southward migration. In this study, three species, Oxytropis nigrescens, O. mertensiana and O. arctica which have a distribution that includes Arctic and Eastern U.S.S.R. and Alaska, were found to have 2n = 16. The distribution of these three species indicates a fairly recent migration from the Old World to the New.

The separation of New World counts into three regions in Figure 101 places all species found in Canada and Alaska in this northern group, although their area of distribution may extend into the United States. All species with the base number 8 are found in the Canada-Alaska section. One species, A. mexicanus DC. (2n = 64) was reported as found in the United States in Ledingham's 1960 paper. Turner (1959) in The Legumes of Texas has given A. mexicanus DC. as a synonym for A. crassicarpus Nutt. which has a chromosome number of 2n = 22. The material used by Ledingham in his 1960 count is now known to have been misidentified at the source. The other count of 2n = 64 by Tschechow in 1935 has not been explained. It is likely that a similar misidentification of the species occurred in his study and that the true number is 2n = 22.

In order to assess the significance of the distinct chromosome number split in Astragalus, it is necessary to consider briefly some other members of the Leguminosae.

The three subfamilies of the Leguminosae are generally ranked in order from the most primitive to the most advanced as follows:

Mimosoideae, Caesalpinioideae, and Papilionoideae. The following table from Atchison (1951) points to a "linear trend" in the evolution of four of the factors considered important in the development of the Leguminosae.

TABLE III: Morphological comparison of the subfamilies of the Leguminosae (data from Atchison, 1951, Table 2).

Character	Mimosoideae	Caesalpinioideae	Papilionateae
Stamens	Free	Free and united	Mostly united
Flowers	Actinomorphic	Intermediate	Zygomorphic
Aestivation of sepals	Valvate	Imbricate and ascending	Imbricate and descending
Habit	Woody	Mostly woody	Woody and herbaceous

It would be foolish to make any statements about the legume family's evolution without a thorough knowledge of the tropical genera which compose the greatest part of this family. The work of Atchison (1951) and Turner and Fearing (1959) must be referred to for information on this subject.

The Mimosoideae appear to be a relatively uniform subfamily. Both Atchison, and Turner and Fearing agree that the origin of the Papilionoideae was probably not from this group but from the Caesalpinioideae. Of the eighteen genera of Mimosoideae listed in Darlington and Wylie (1955), fourteen have n = 13 or 14. These present numbers are thought by Atchison to have arisen by ploidy of some sort at an early time from n = 6 and n = 7 ancestors. It is difficult to see why Atchison proposed n = 6 and n = 7 ancestors when there are no counts in the subfamily to support this idea. Three genera have a haploid number of 8, but no genera have

6 or 7. She cites the pod character as the only "indisputable link" between the Mimosoideae and the other two subfamilies.

The Caesalpinioideae is made up of a number of tribes with a somewhat variable chromosome number. The low 7's and 8's are common haploid numbers along with the higher 10's, 11's, 12's and 14's. The following quotation from Turner and Fearing (1959) states concisely the relationship of the Papilionoideae to this subfamily:

> The absence of genera with base numbers of x = 9 in the Caesalpinioideae and their rarity in the Papilionoideae (except for the Sophoreae and the Podylareae, discussed above) lends credibility to the hypothesis that 2 major chromosomal lines emerged from the subfamily Caesalpinioidea, one on a base of x = 10 and 11, giving rise to the Dalbergeae and the Phaseoleae, and the other on a base of x = 8, giving rise to the remaining tribes on a base of x = 7, 6, or 5, by aneuploid loss, and to the 9-line Sophoreae and Podylareae, by aneuploid gain.

In this same paper, Turner and Fearing presented a table showing the proposed phylogenetic trends in the Leguminosae exclusive of the Mimosoideae. This scheme has been reproduced here as Figure 104. Of greatest significance in relation to the problem of the genus Astragalus is the proposed split of the tribe Galegeae in accordance with the variable chromosome numbers of x = 5, 6, 7, 8, 10, and 11. Atchison (1951) had earlier suggested that the Galegeae with the higher chromosome numbers might well be placed within the tribe Dalbergieae. The data obtained for the genus Astragalus supports this proposed split of the Galegeae. However, the numbers x = 12 and 13 would be added to the higher numbered Galegeae on Turner and Fearing's table. Not enough is known by the author of the other tribes of the Papilionoideae with the base numbers of 10, 11, and 12 to evaluate the interrelationships among these taxa or the proposal of the inclusion of part of the Galegeae with

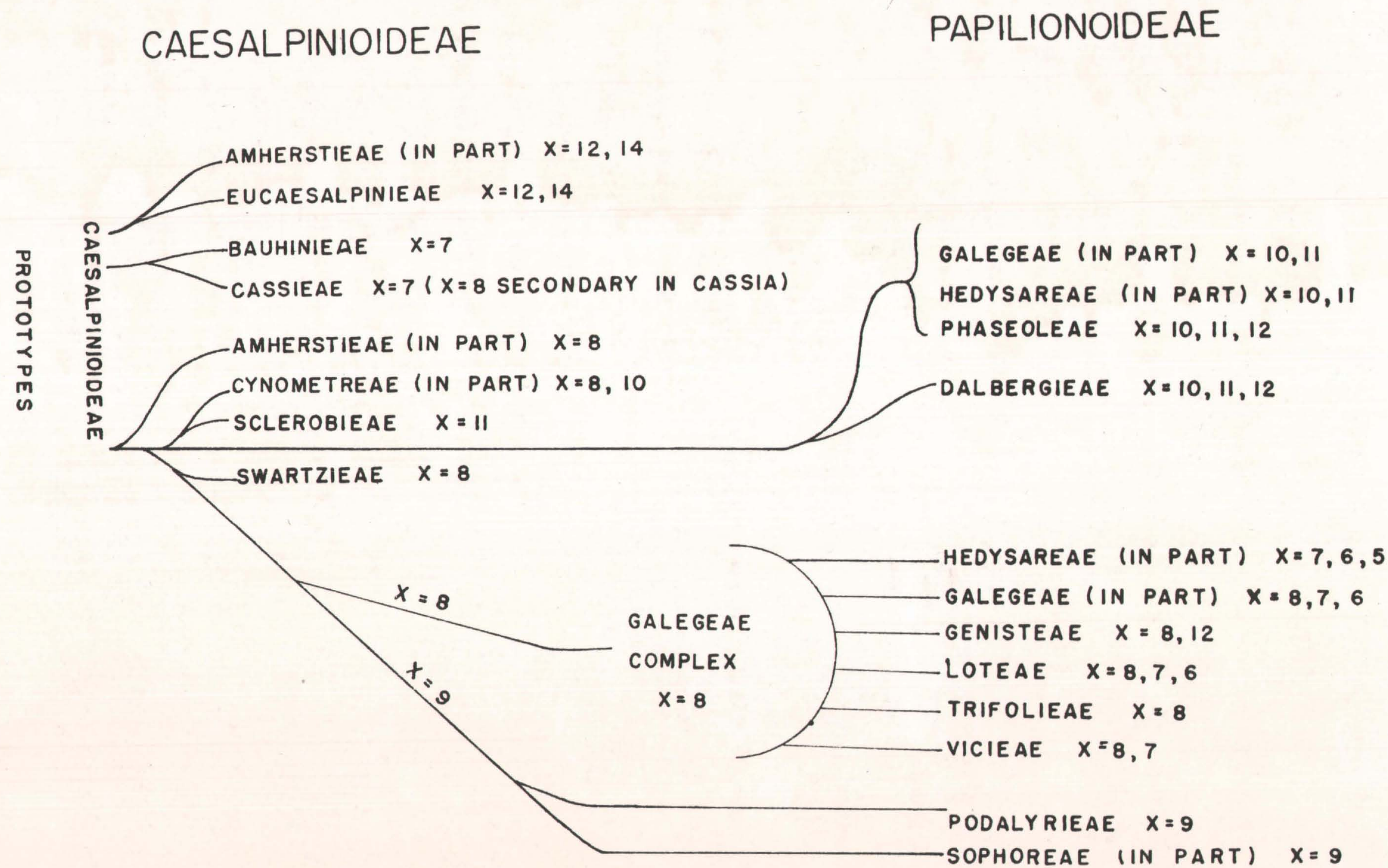


FIGURE 104. Diagram showing hypothetical phyletic lines within the Leguminosae (excluding the Mimosoideae) as determined from chromosomal evidence. (data from Turner and Fearing, 1959, FIG. 28).

Dalbergieae. One thing is obvious, however. If the present tribe Galegeae were split in accordance with the chromosome numbers, the Old and New World species of Astragalus would be in different tribes and, necessarily, in different genera.

The complete absence of species with the base number 9 and the single species with n = 10 in the genus Astragalus suggests that there have been separate but parallel evolutions in the New and Old World species. The geographic distinctness of the two groups gives added significance to the chromosome number difference. The morphological similarities between the two geographic groups can likely be explained by selective adaptation to similar environmental conditions in both the New and the Old World.

If 12 is considered the average base number of the New World group of Astragalus and 8 the most common number in the Old World, the question arises of whether or not the real base number for the genus could be 4.

In an interesting statistical study made by Wanscher (1934), chromosome counts of 2563 species, including 38 families of Dicotyledons and 6 families of Monocotyledons, were analysed as to the frequencies of the base numbers from 3 to 24 in each of the two sections.

In the Dicotyledons, 8 and 12 appeared as the most frequent numbers on a bimodal curve. Wanscher took the difference, 4, between these two peaks as being significant. He concluded that the chromosome numbers of the higher plants have originated from numbers belonging to a four system, even though very few species have been recorded with 2n = 8. The two schemes proposed by Wanscher have been adapted as follows for somatic numbers:

Scheme 1:

$$
\begin{tikzcd}
 & & 16(4_4) & & \\
8(4_2) \arrow[r] & 16(4_4) \arrow[ur] \arrow[dr] & \text{x} \arrow[r] & 24(4_6) \arrow[r] & 24(12_2) \\
 & & 32(4_8) & &
\end{tikzcd}
$$

At an early time, the diploid 8 became doubled to give tetraploids and octoploids. Hybridization between these polyploids gave rise to hexaploids. Pairing could only occur in the hexaploid providing that no considerable variation in the chromosomes of the parent species had occurred. It is difficult to accept this origin for a hexapoloid. The only point in favor of this explanation of origin is that it assumes the loss of diploid 8's early in the evolutionary history. There are no recorded counts of 2n = 8 in the family Leguminosae. This means either that the base number of the family is not 4, or that the low haploid number has been eliminated at an early time in favor of polyploid numbers.

Scheme 2:

$$
\begin{tikzcd}
 & 8(4_2) & & & \\
8(4_2) \arrow[ur] \arrow[dr] & \text{x} \arrow[r] & 12(4_3) \arrow[r] & 24(4_6) \arrow[r] & 24(12_2) \\
 & 16(4_2) & & &
\end{tikzcd}
$$

This derivation shows the formation of a triploid followed by alloploid doubling to give the hexaploid. Here, variation in the chromosome structure of the parent species would be an advantage so that the amphidiploid would immediately have regular pairing of the two sets of 12 chromosomes. This type of number change would seem more plausible than that suggested in Scheme 1. However, the second sequence would mean the participation of diploid 8's at a more recent time in the evolutionary history of the genus than is thought likely.

Towards the completion of the research for this thesis, a count of 2n = 16 was made for _A. mongholicus_ Bunge. Further work on this species yielded a root tip squash with only 8 chromosomes. At first it was thought that the material might be something other than _Astragalus_. Fortunately, the slide had many excellent division figures which showed a character that enabled identification of the material as a haploid of _A. mongholicus_. Figures 98, 99, and 100, show the chromosome relationship clearly. In the diploid cell, a pair of chromosomes which appear to have split in the centromere region during slide preparation are prominent. This gives an appearance of 2n = 18. However, some cells were present which showed the connection of the parts of this chromosome pair and the true number of 2n = 16. In the haploid, almost two thirds of the division figures showed a single chromosome with widely separated parts. This, then, indicated a relationship with the diploid. From this observation, a base number of 8 would seem likely for the Old World species. Study of meiotic division figures would reveal whether or not a possible base of 4 exists, but the rarity of haploid individuals makes this a difficult task. A single chromosome in the haploid set with two non-staining regions was observed. This did not show clearly in the diploid preparations of this species.

Although no deliberate attempt was made to do any work on the chromosome structure of the genus because of the small size of the chromosomes, fifteen other species were noted as having a pair of chromosomes which tended to split at the centromere. These species — _A. aksuense, A. maximowiszii, A. membranaceous, A. expansus, A. illyricus, A. eremospartoides, A. schrenkianus, A. platyphyllus, A. lasiosemius, A. xanthomeloides, A. kahiricus, A. xipholobus,_ _O_. _chiliophylla_, _O_. _sulphurea_ and _O_. _mertensiana_ — all had a chromosome number of 2n = 16. Two other species, _A_. _schahrudensis_ and _A_. _eximius_, were noted to have a pair of chromosomes with two non-staining regions. In counting, the figures which showed the chromosome number most clearly, not the chromosome morphology, were chosen for recording. There may have been other occurrences of these two types of chromosomes in the species studied which were not recorded.

As far as is known, neither the split chromosome pair nor the chromosome pair showing the two non-staining regions has been recorded in any of the New World species. A greater attention to chromosome morphology may make possible the tracing of a relationship between the Old World and New World groups.

Considering the difficulties involved in both of the schemes suggested by Wanscher and the evidence that there is a haploid set of 8 in an Old World species, it seems unlikely that the 8 and the 12 chromosome numbers in _Astragalus_ have been derived from an ancestor with a base number of 4.

If there were two separate parallel evolutions in _Astragalus_, the center of origin of the Old World 8's was almost certainly Central Asia, while the center of origin for the New World 11, 12, and 13's was likely in western North America. If either the New World center or the Old World center had been in the southern hemisphere, the genus would most certainly be represented in Australia and other southern countries. _Oxytropis_, with a more restricted and more northern distribution, is likely an offshoot from Old World _Astragalus_. Its absence in more southern parts of the world could be explained in two ways. Either this genus originated in the North in comparatively recent times and has not yet extended its area as far south as that of Astragalus, or there is some unknown factor in the nature of the genus Oxytropis which excludes its existance in the hotter desert regions of the south.

The chromosome number character in Astragalus has been shown by this study to be generally constant. B. L. Turner and his associates have done extensive work on chromosome numbers in the Leguminosae. Turner and Fearing (1959) used this character as a basis for the phylogenetic scheme of the Caesalpinioideae and the Papilionoideae (Fig. 104). The work on Astragalus chromosome numbers places this genus in the phylogenetic scheme as suggested by the previous legume counts used by Turner and Fearing. This study, therefore, supports the validity of using chromosome numbers in taxonomy, at least, in the taxonomy of this family. Biochemical methods of taxonomy are now being used by Turner et al. to corroborate the ideas of phylogeny in the Leguminosae that were first suggested by chromosome number studies. Since there appear to be no external morphological characters exclusive to either of the Astragalus groups, support for the separation of the genus is most likely to be found by using the methods of biochemistry or by examining the internal morphology of members of the genus. It is hoped that eventually there will be sufficient evidence for the separation of the genus Astragalus to satisfy even the most dubious taxonomist.

SUMMARY

Eighty-four new chromosome counts in *Astragalus* and *Oxytropis* and 16 counts of species in these two genera which have previous published counts (3 of which differ from the previous counts) are reported here. The known counts in the two genera are compiled and graphed to show the distribution of chromosome numbers in the Old World and in the New World. This summary shows the dominance of the base number 8 in the Old World species of *Astragalus* and of the base numbers 11, 12 and 13 in the New World species. The constancy of these numbers in the 282 species whose chromosome numbers are known gives support to the suggested splitting of the genus *Astragalus* into two separate genera on the basis of chromosome number and geographic distribution, (Ledingham, 1960). Postulations are made on the possible phylogeny of *Astragalus* and *Oxytropis* and on the place of these genera in the Leguminosae. The derivation of the base numbers 8 and 12 in the two groups is discussed. The difficulties in obtaining both of these numbers from an ancestor with a base number of 4, and the finding of a haploid in an Old World species which seemed to have a haploid set of 8, lead the author to suggest separate parallel evolutions in the two *Astragalus* groups.

BIBLIOGRAPHY

Alston, R. E. and Irwin, H. S. 1961. The comparative extent of variation of free amino acids and certain "secondary" substances among Cassia species. Am. J. Botan. 48: 35-39.

Andrews, E. C. 1914. The development and distribution of the natural order Leguminosae. J. and Proc. Royal Soc. of New South Wales. 48: 333-407.

Atchison, Earlene. 1949. Studies in the Leguminosae. IV. Chromosome numbers and geographical relationships of miscellaneous Leguminosae. Jour. Elisha Mitchell Soc. 65: 118-122.

————————. 1951. Studies in the Leguminosae. VI. Chromosome numbers among tropical woody species. Am. J. Botan. 38: 538-546.

Axelrod, Daniel I. 1959. Poleward migration of early angiosperm flora. Sci. 130: 203-207.

Barneby, R. C. 1952. A revision of the North American species of Oxytropis DC. Proc. Calif. Acad. Sci. 27: 177-309.

Baroni, Eugenio. 1932. Guida botanica d'Italia. Bologna. 659 pp.

Berger, C. A., Witkus, E. R. and McMahon. 1958. Cytotaxonomic studies in the Leguminosae. Bull. Torr. Botan. Club. 85: 405-415.

Berry, Edward W. 1927. Links with Asia before the mountains brought aridity to the Western United States. Scientific Monthly.

Birdsong, B. A., Alston, R. and Turner, B. L. 1960. Distribution of canavanine in the family Leguminosae as related to phyletic groupings. Can. J. Botan. 38: 499-505.

Braun-Blanquet, Josias. 1923. L'origine et le développement des flores dans le Massif Central de France.

Brooks, C. E. P. 1926. Climate through the ages. Ernest Benn Ltd. London.

Bubani P. 1897-1901. Flora Pyrenaea. Mediolani. 555, 718, 435, 456 pp.

Burbidge, Nancy. 1960. The phytogeography of the Australian region. Aust. J. Botan. 8. 75-211.

Cain, S. A. 1944. Foundations of plant geography. Harper and Bros. New York.

Camp, W. H. 1947. Distribution problems in modern plants and the problem of ancient dispersals. Ecol. Mon. 17: 149-183.

————————. 1951. Biosystematy. Brittonia 7: 113-127.

Campbell, D. H. 1944. Relations of the temperate floras of North and South America #2. Proc. Calif. Acad. Sci. 25: 139-146.

Cave, M. S. ed. 1958-1960. Index to plant chromosome numbers. Calif. Botan. Soc.

Coutinho, A. X. P. 1939. Flora de Portugal. Ed. 2 dir. pelo R. T. Palhinha. Lisbon. 938 pp.

Croizat, Leon. 1952. Manual of phytogeography. Junk. The Hague. 558 pp.

————————. 1958. Panbiogeography. Vol. 1, IIa, IIb. Caracas.

Darlington, C. D. and Wylie, A. P. 1955. Chromosome atlas of flowering plants. Allen and Unwin. London.

Debeaux, J. O. 1888. Synopsis de la flore de Gibraltar. Actes Soc. Linn. Bordeaux 42. 121-378.

DeCandolle, A. 1802. Astralogia. Joann. Bapt. Garnery. Paris.

du Toit, A. L. 1937. Our wandering continents. Oliver and Boyd. Edinburgh.

Eig, A. 1955. Systematic studies on Astragali of the Near East. Weizmann Science Press of Israel. Jerusalem.

Ewan, Joseph. 1944. The perennial southwestern Datura and the validity of Matthew's hypothesis in plant geography. Proc. Calif. Acad. Sci. 25: 235-244.

Fedchenko, O. A. 1903. Flora of Pamir. Acta Horti Petropolitani. 21.

Frahm - Leliveld, J. A. 1957. Observations cytologiques sur quelques Legumineuses tropicales et subtropicales. Revue de cytologie et de biologie vegetales. 18.

————. 1958. Some considerations on chromosome dynamics in relation to taxonomy of the flowering plants I. Proc. Koninkl Nederl. Akademie van Wetenschappen. Amsterdam. Series C. 61.

Good, R. 1953. The geography of the flowering plants. Longmans, Green. London.

Goodspeed, T. H. 1954. The genus Nicotiana. Chronica Botanica. Waltham, Mass.

Griffin, J. B. 1960. Some prehistoric connections between Siberia and America. Sci. 131.

Hammond, H. D. 1947. Study of taxonomic relationships by the photron'er serological method. Master's thesis, unpub. Rutgers Univ.

————. 1952. Systematic serological studies in the Ranunculaceae. Doctoral thesis, unpub. Rutger's Univ.

Head, S. Conrade. 1957. Mitotic chromosome studies in the genus Astragalus. Madrono. 14: 95-106.

Hegi, Gustav. 1924. Illustrierte Flora von Mittel-Europa. Munich. Vol. 4. Part 3.

Helmsley, W. B. and Pearson, H. H. W. 1904. The flora of Tibet or High Asia. Jour. Linn. Soc. (Botan.) 35: 124-265.

Heslop-Harrison, J. 1953. New concepts in flowering plant taxonomy. Heinemann. London.

Holmes, A. 1953. Principles of physical geology. Thos. Nelson and Sons. Toronto.

Hulten, Eric. 1937. Outline of the history of Arctic and boreal biota during the Quaternary period. Stockholm.

————. 1958. The amphi-atlantic plants and their phytogeographical connections. Almquist and Wiksell. Stockholm.

Irwin, H. S. and Turner, B. L. 1960. Chromosomal relationships and taxonomic considerations in the genus Cassia. Am. J. Botan. 47: 309-318.

Johnson, M. A. 1954. The precipitin reaction as an index of relationship in the Magnoliaceae. Serological Museum Bull. 13.

Johnston, Ivan M. 1940. The floristic significance of shrubs common to North and South America deserts. Jour. Arn. Arb. 21: 356-363.

————. 1947. Astragalus in Argentina, Bolivia and Chile. Jour. Arn. Arb. 28: 336-409.

Jones, Marcus E. 1923. Revision of North-American species of Astragalus. Salt Lake City. Utah.

Kolbe, R. W. 1957. Fresh-water diatoms from Atlantic deep-sea sediments. Sci. 126: 1053-1056.

Komarov, B. L. 1946. Flora of the U.S.S.R. Vol. XII. Leningrad. 915 pp.

————. 1948. Flora of the U.S.S.R. Vol. XIII. Leningrad. 588 pp.

Köppen, W. and Wegener, A. 1924. Die Klimate der geologischen Vorzeit. Berlin.

Kreuter, Erich. 1929. Chromosomenstudien bei den Galegeen. Berichte der Deutschen Botanischen Gesellschaft. 47: 99-101.

————. 1930. Beitrag zu karyologischsystematischen Studien an Galegeen. Planta. 2: 1-44.

Kryshtofovich, A. N. 1929. Evolution of the tertiary flora in Asia. New Phyt. 28: 303-312.

Ledingham, G. F. 1957. Chromosome numbers of some Saskatchewan Leguminosae with particular reference to Astragalus and Oxytropis

Can. J. Botan. 35: 657-666.

-----------. 1958. Chromosome numbers in Astragalus. Proc. Genet. Soc. Can. 3: 15-18.

-----------. 1960. Chromosome numbers in Astragalus and Oxytropis. Can. J. Genet. Cytol. 2: 119-128.

Lindberg, Harold. 1931. Itinera Mediterranea. Acta Societatis Scientiarum Fennicea. 1:2. 178 pp.

Lindroth, Carl H. 1957. The faunal connections between Europe and North America. John Wiley & Sons. New York. 334 pp.

----------. 1960. Is Davis Strait - between Greenland and Baffin Island - a floristic barrier? Botaniska Notiser 113: 129-140.

Mirov, N. T. 1960. Geography of Russia. John Wiley & Sons. New York.

Palhinka, R. T. 1939. Flora de Portugal. Bertrand. Lisbon.

Post, G. E. 1932-33. Flora of Syria, Palestine and Sinai. Oxford. 639, 966 pp.

Rechinger, K. H. 1948. Reliquiae Samuelssonianae. Arkiv. Bot. 1.

----------. 1957. Leguminosae, in Koie, M. and Rechinger, K. H. : Symbolae Afghanica, III. Biol. Skr. Dan. Vid. Selsk. 9, No. 3.

-----------. Dulfen, H. and Patzak. 1958-59. Sirjaevii fragmenta astragalogica I - XII. Osterreichische Akademie der Wissenschaften. Vienna.

Rechinger, K. H. fil. 1949. Zur Flora von Cypern. Arkiv. f. Bot. Ser. 1, 9.

---------. 1951. Zur Flora der Türkei. Arkiv. f. Bot. Ser. 2, 1. 513-543.

Reiche, Karl. 1907. Die Vegetation der Erde VIII. Grundzüge der Pflanzenverbreitung in Chile. Leipzing.

Rikli, M. 1943. Das Pflanzenkleid der Mittelmeerländer. Vol. 1-3. Hans Huber. Berne. 436, 1093, 1418 pp.

Ridley, Henry N. 1930. The dispersal of plants throughout the world. Reeve. Ashford, Kent.

Riley, H. P. and Bryant, T. R. 1961. The separation of nine species of the Iridaceae by paper chromatography. Am. J. Botan. 48: 133-137.

Runcorn, S. K. 1959. Rock magnetism. Sci. 129:1002-1012.

Senn, Harold A. 1938. Chromosome number relationships in the Leguminosae. Bibliographia Genetica XII. The Hague.

Sirjaev, G., and Rechinger, K. H. fil. 1951. Astragali et Onobrychides novi orientales. Ann. Nat. Mus. Wien 58.

Sporne, K. R. 1959. On the phylogenetic classification of plants. Am. J. Botan. 46: 385-394.

Stebbins, G. L. 1950. Variation and evolution in plants. New York.

----------. 1951. Natural selection and the differentiation of angiosperm families. Evol. 5: 299-324.

Szymkiewicz, Dezydery. 1934. Une contribution statistique a la geographie floristique. Acta Soc. Bot. Poloniae. 11: 294-265.

------------. 1936. Seconde contribution statistique a la geographie floristique. Acta Soc. Bot. Ploniae. 13: 271-292.

------------. 1937. Przyczynki do geografii roslin. Kosmos 61; 1-15.

Täckholm, Vivi. 1956. Student's Flora of Egypt. Cairo.

Takhtajian, A. L. 1954. Origins of angiospermous plants (a translation from Russian). Am. Instit. Biol. Sci. Washington.

Tischler, G. 1938. Pflanzliche Chromosomenzahlen IV. Tab. Biol. 16: 162-192.

Turner, B. L. 1955. Chromosome numbers in the genus *Sesbania* (Leguminosae):

Evidence for a conservative treatment. Rhodora 57: 213-218.

----------. 1956. Chromosome numbers in the Leguminosae I. Am. J. Botan. 43: 557-581.

----------. 1958. Chromosome numbers in the genus Krameria : evidence for familial status. Rhodora 60: 101-106.

----------. 1959. The legumes of Texas. Univ. Texas Press. Austin.

----------, and Fearing, O. S. 1959. Chromosome numbers in the Leguminosae II: African species, including phyletic interpretations. Am. J. Botan. 46: 49-57.

Uhl., C. H. 1961. The chromosomes of the Sempervivoideae (Crassulaceae). Am. J. Botan. 48: 114-123.

van der Pijl. L. 1956. Classification of the leguminous fruits according to their ecological and morphological properties. Proc. Neder. Akad. C. 301-313.

-----------. 1961. Ecological aspects of flower evolution II. Zoophilous flower classes. Evol. 15: 44-59.

von Engeln, O. D. and Caster, K. E. 1952. Geology. McGraw-Hill. New York.

Wanscher, J. H. 1934. The basic chromosome number of the higher plants. New Phytol. 33: 101-126.

Ward, F. K. 1935-37. The geography and botany of Tibet. Jour. Linn. Soc. Bot. 239-265.

Wulff, E. V. 1937. Essay on dividing the world into phytogeographical regions according to the numerical distribution of species. Papers on the Taxon. and Geography of Plants. Leningrad. Series 1, no. 2 315-368.

Wulff, E. V. 1950 (repub. from 1943). An introduction to historical plant geography. Chronica Botanica. Waltham, Mass.

APPENDIX A

Photographs selected from the collection

of G. F. Ledingham

to show the varying forms and habitats of some species of

Astragalus and *Oxytropis*.

A. platyraphis Fisch.

"In Nature's infinite book of secrecy
A little I can read."

WILLIAM SHAKESPEARE - Antony
and Cleopatra. Act I. Sc. 2.

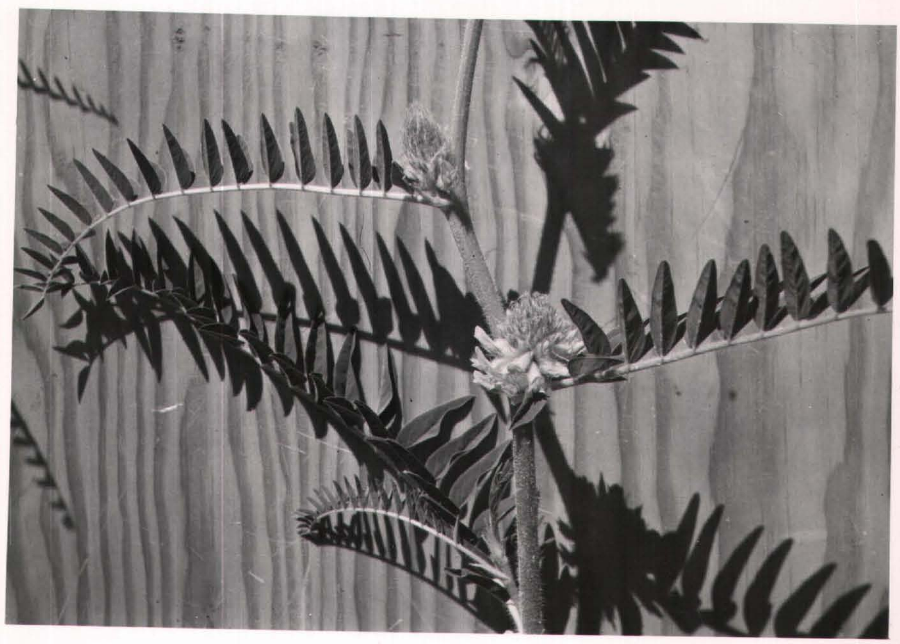


FIG. A - 1. A. alopecuroides L. (2n = 16). Inflorescences axillary on upper part of erect 3 - 4 foot stems. Habitat on mountain slopes, Mediterranean Europe to Turkestan.

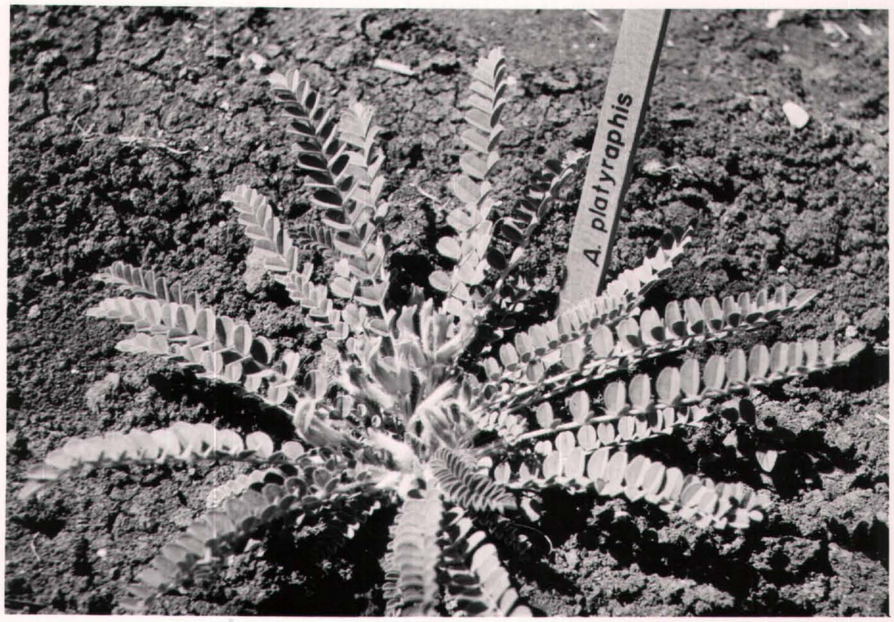


FIG. A - 2. A. platyraphis Fisch. (2n = 16). Inflorescences on short peduncles, plant acaulescent. Habitat on dry hills or in sandy places, Palestine, Syria and Iraq.

FIG. A - 3. A gilviflorus Sheld. = A. triphyllus Pursh. (2n = 24).

FIG. A - 4. Typical habitat of A. gilviflorus on a dry eroded slope, Big Muddy Valley, Saskatchewan.

FIG. A - 5. A spatulatus Sheld. (2n = 24).

FIG. A - 6. A. spatulatus growing in its typical habitat on a high rocky knoll, Cypress Hills, Saskatchewan.

FIG. A - 7. O. splendens Dougl. (2n = 16).

FIG. A - 8. Typical habitat of O. splendens in open grasslands, foothills west of Calgary, Alberta.

FIG. A - 9. A. vexilliflexus Sheld. (2n = 22), growing in barren rocky places in the foothills west of Calgary, Alberta.

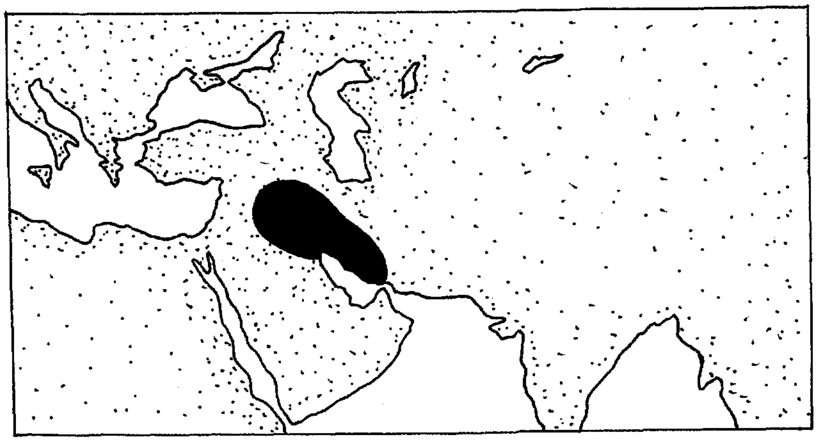
FIG. A - 10. A. kentrophyta Nutt. (2n = 24), growing on dry sandy bank above the Milk River, Alberta.

APPENDIX B

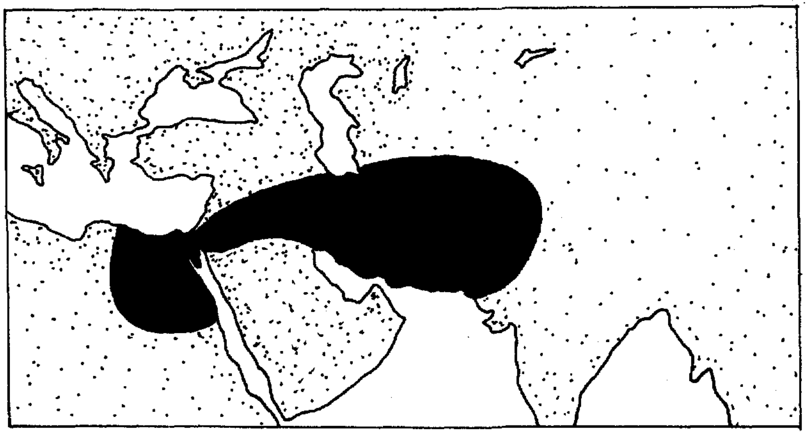
Geographical distribution of species of

Astragalus and *Oxytropis*

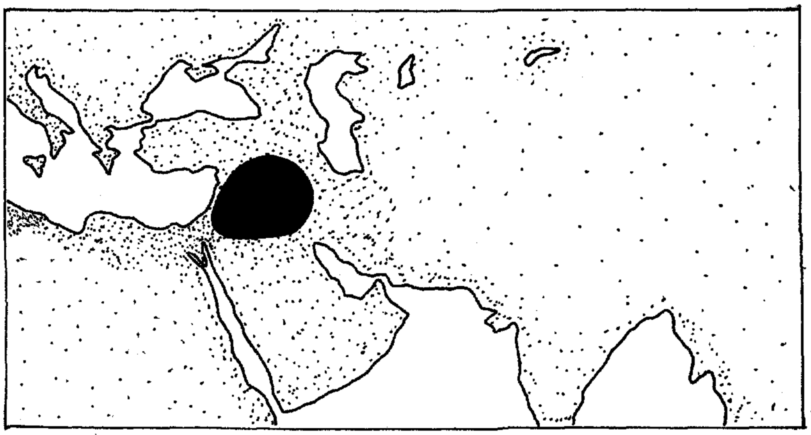
whose chromosome numbers are reported in this thesis.



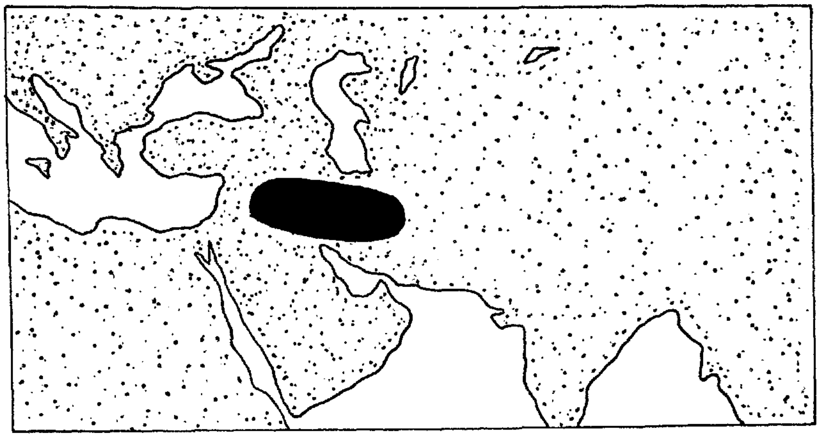
MAP I *A. mossulensis*



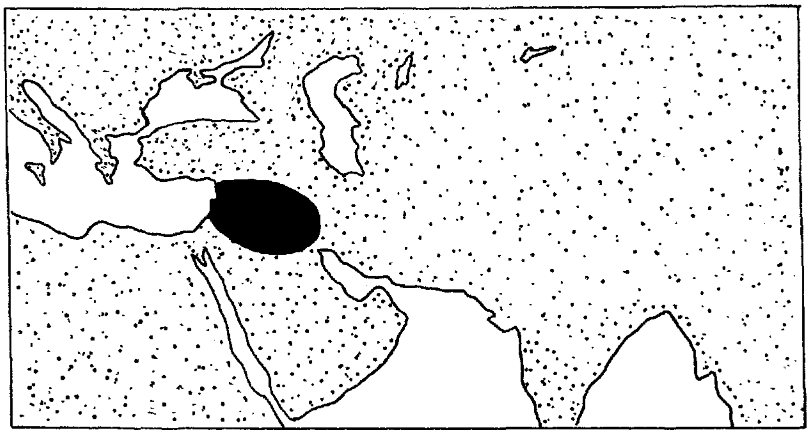
MAP 2 *A. kahiricus*



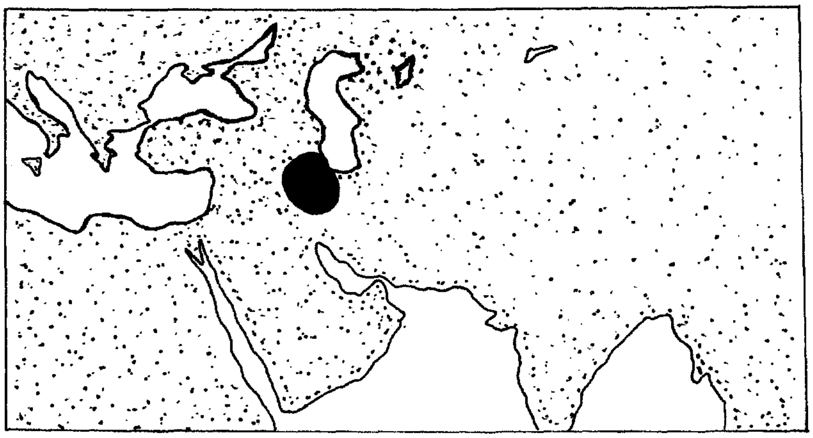
MAP 3 *A. palmyrensis*



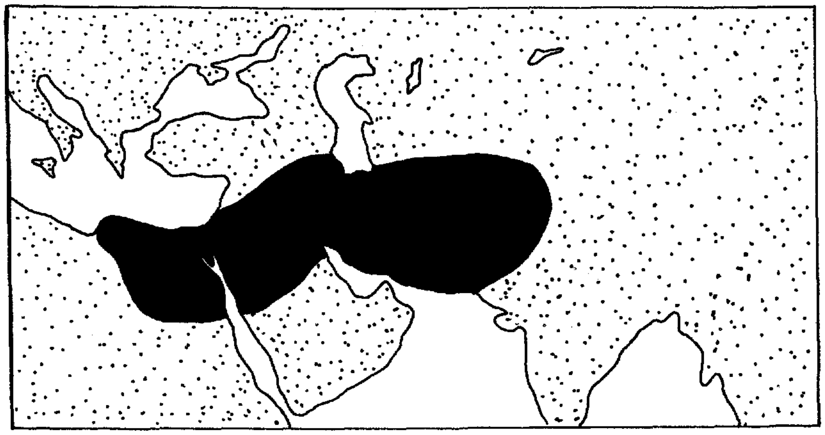
MAP 4 *A. macropelmatus*



MAP 5 *A. platyrahphis*

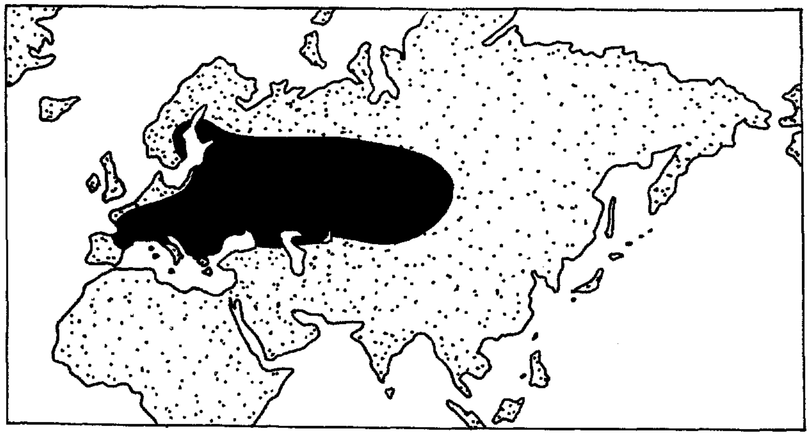


MAP 6 *A. finitimus*

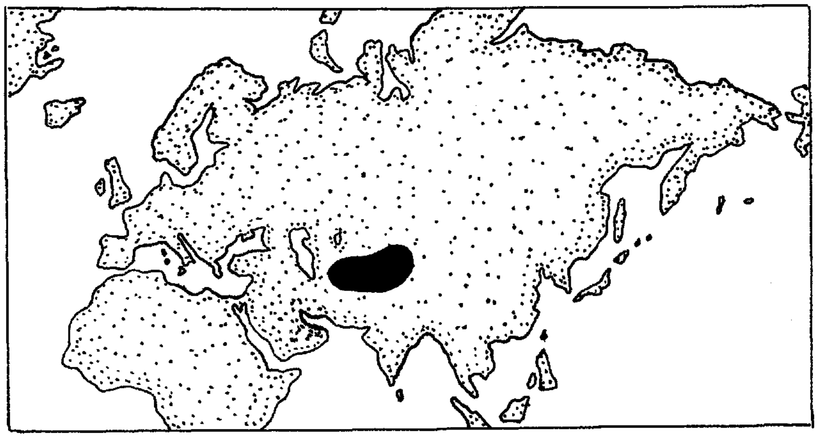


MAP 7 *A. tribuloides*

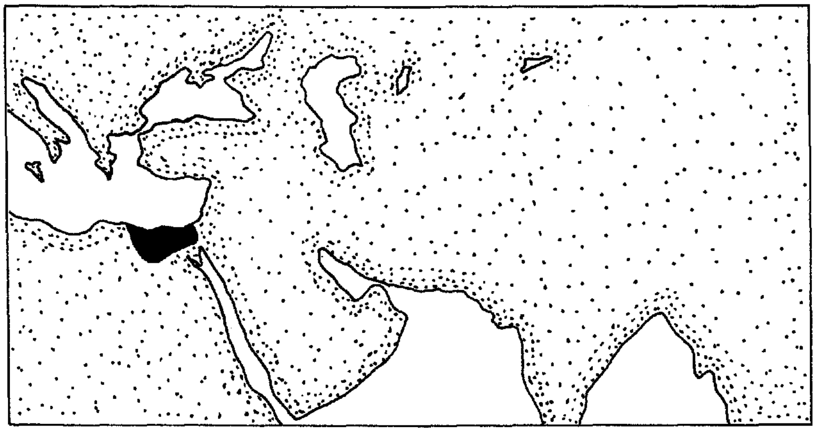
MAP 8 *A. corrugatus*



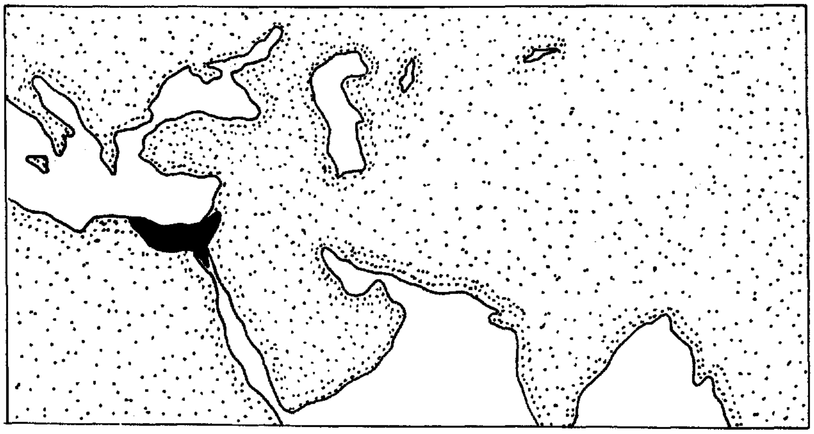
MAP 9 *A. mucronatus*



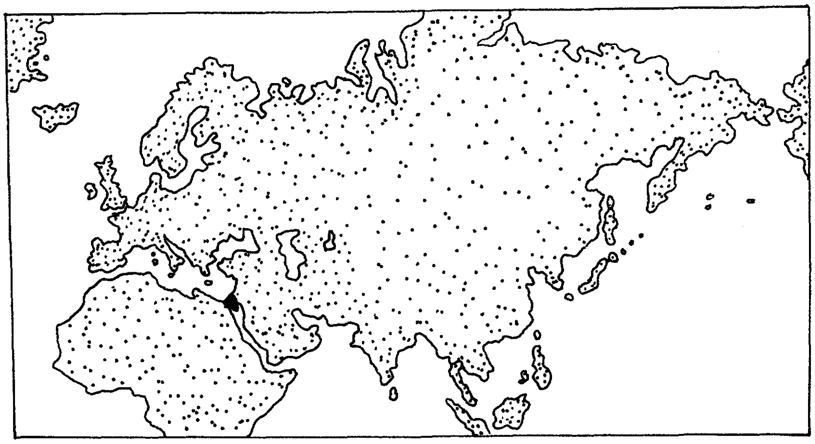
MAP 10 *A. campylotrichus*



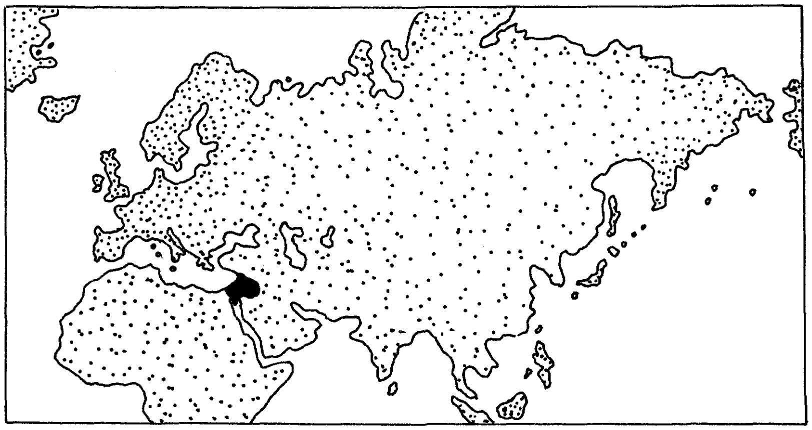
MAP 11 *A. leucacanthus*



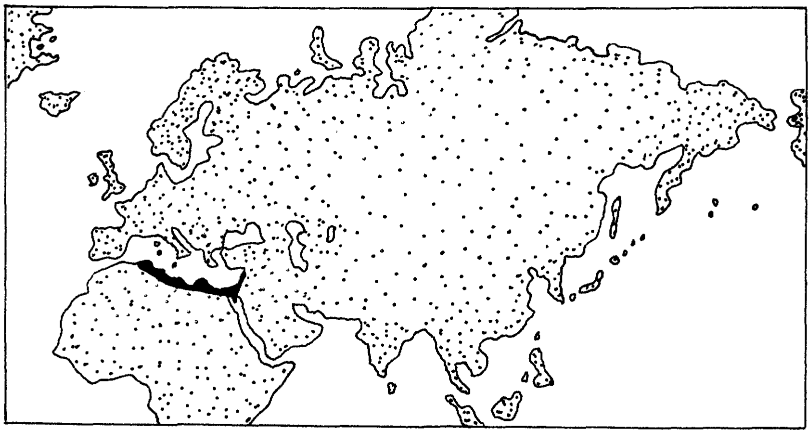
MAP 12 *A. hispidulus*



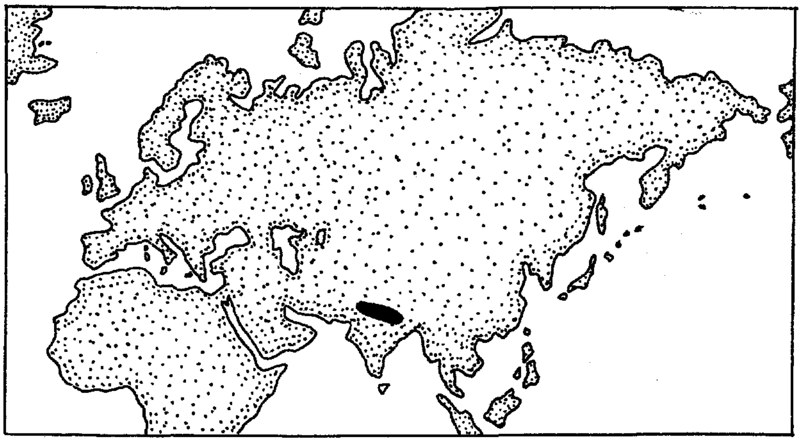
MAP 13 *A. sieberi*



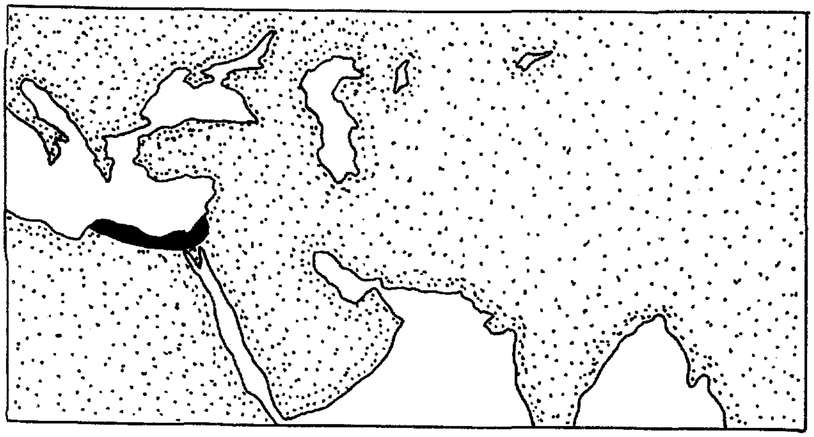
MAP 14 *A. bombycinus*



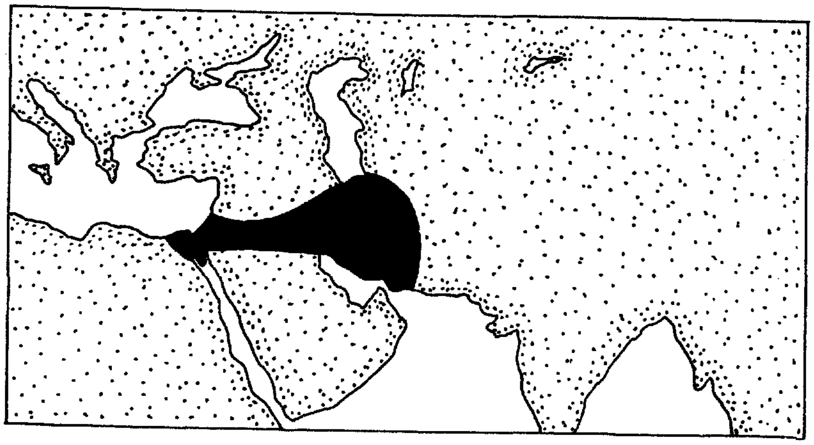
MAP 15 *A. peregrinus*



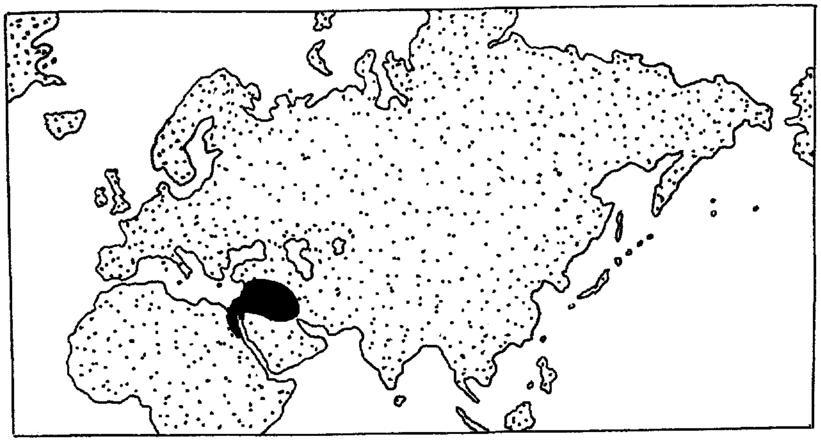
MAP 16 *A. chlorostachys*



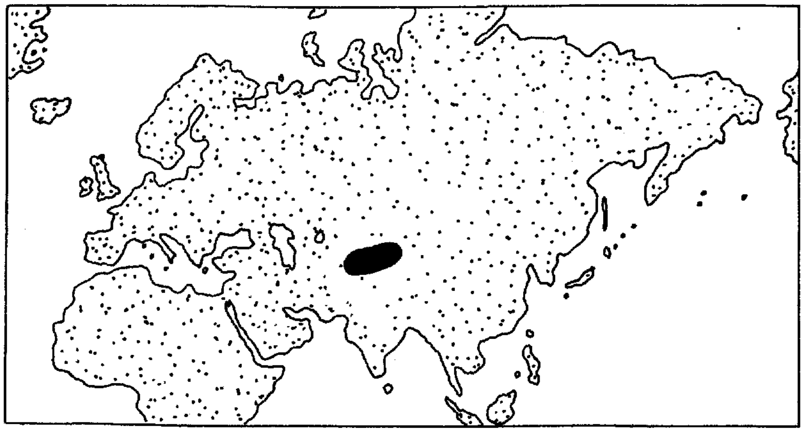
MAP 17 *A. alexandrinus*



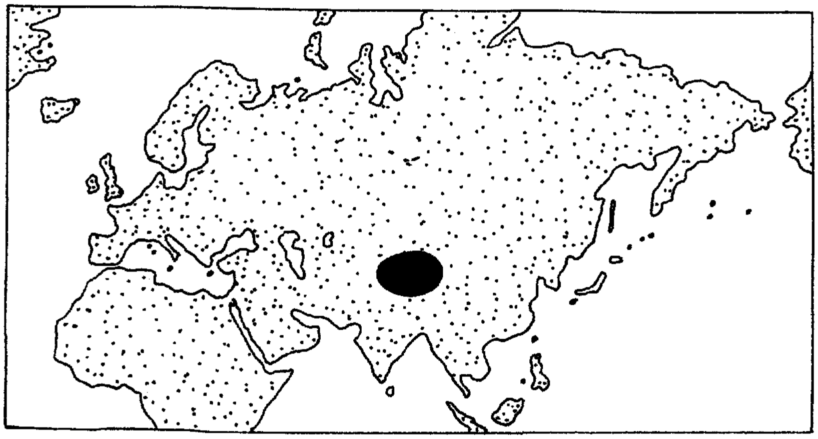
MAP 18 *A. gyzensis*



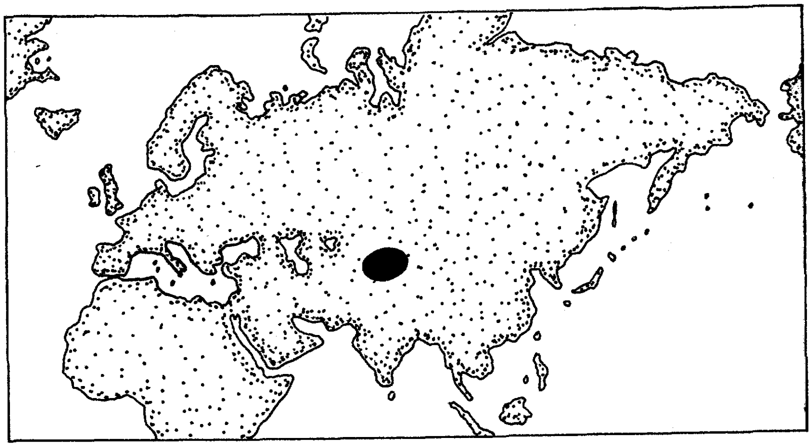
MAP 19 *A. schimperi*



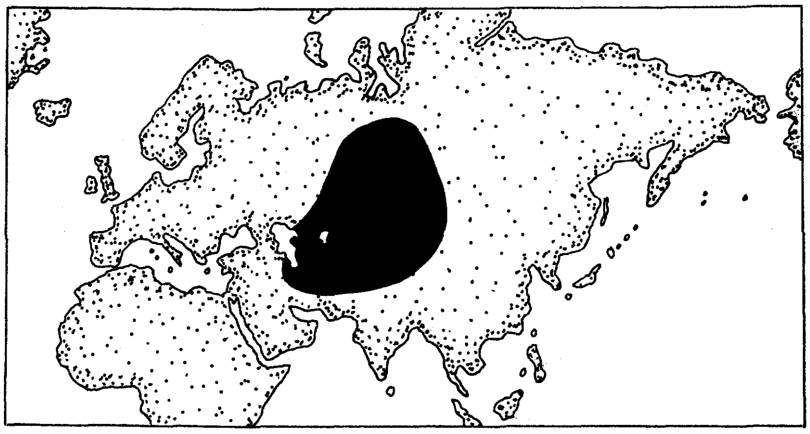
MAP 20 *A. scheremetevianus*



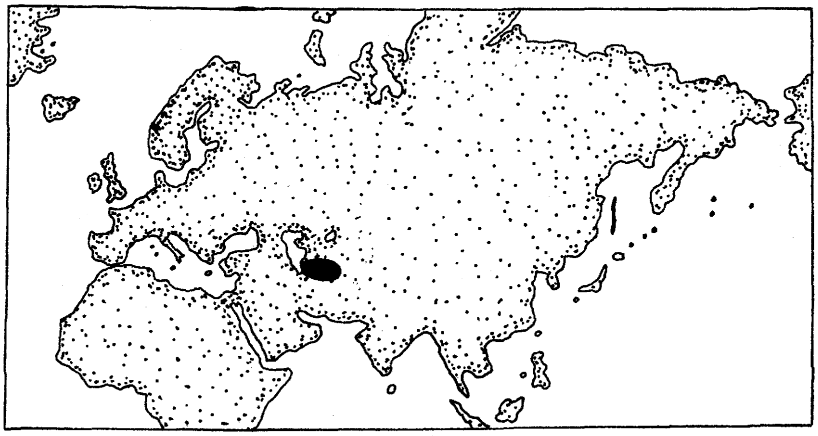
MAP 21 *A. heterodontus*



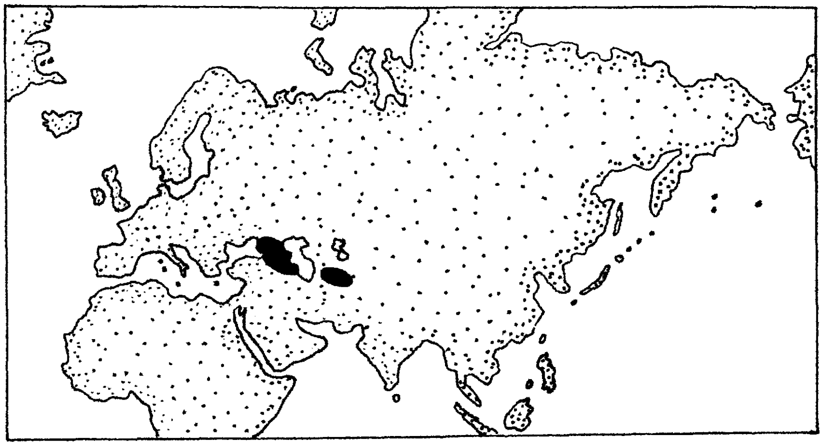
MAP 22 *A. schugnanicus*



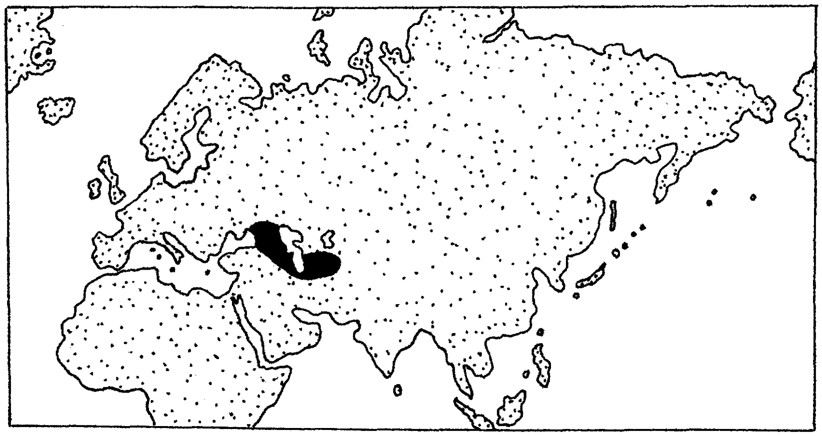
MAP 23 *A. alopecias*



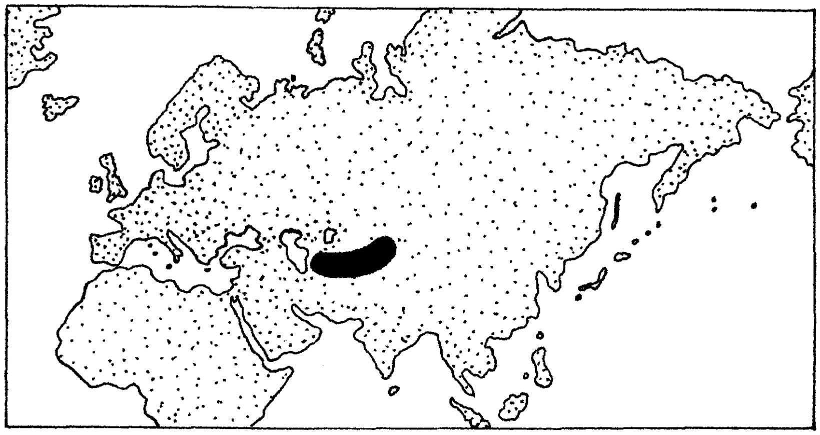
MAP 24 *A. ackerbergensis*



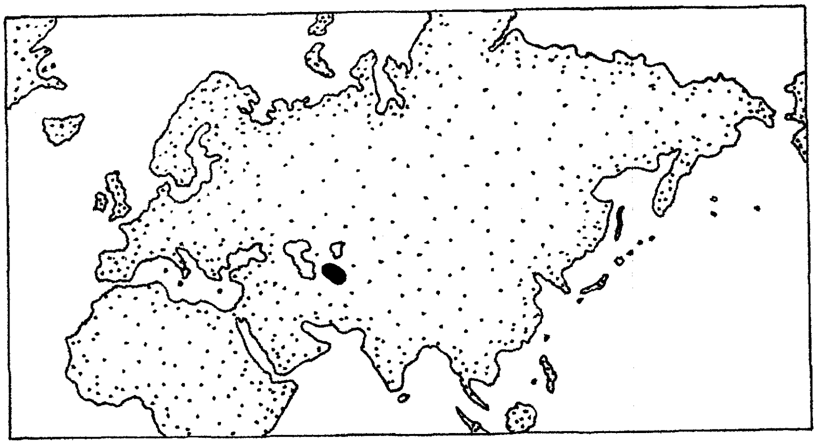
MAP 25 *A. maximowiszii*



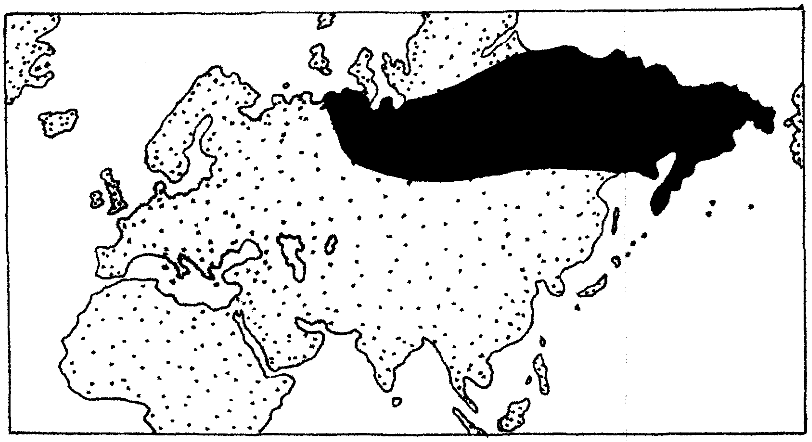
MAP 26 *A. brachypetalus*



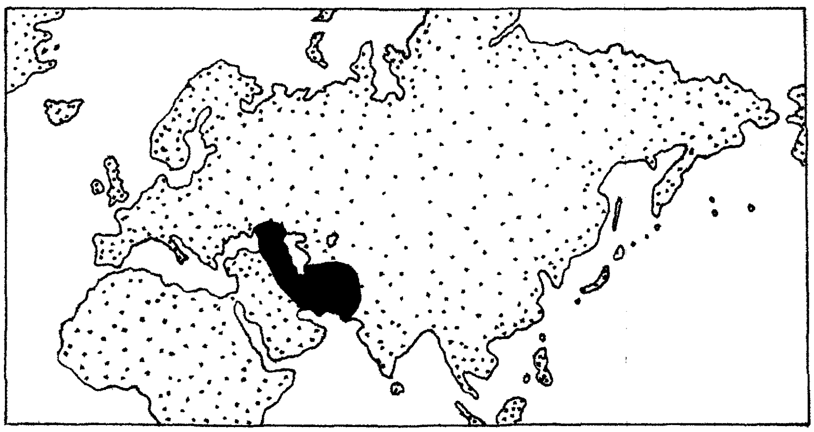
MAP 27 *A. schmalhausenii*



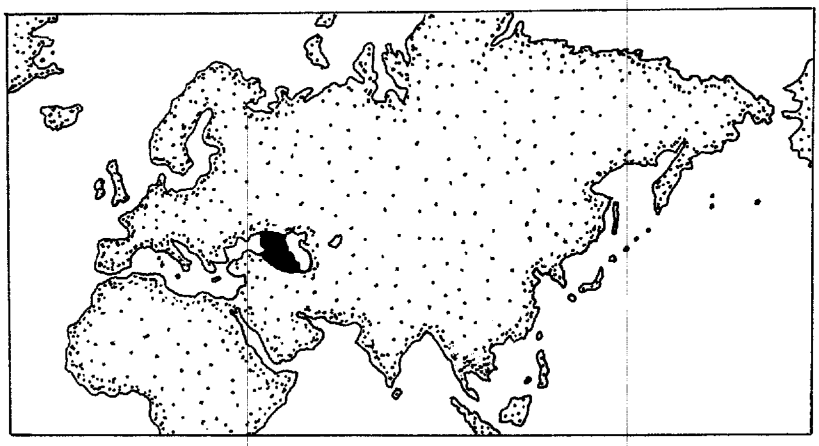
MAP 28 *A. longipetiolatus*



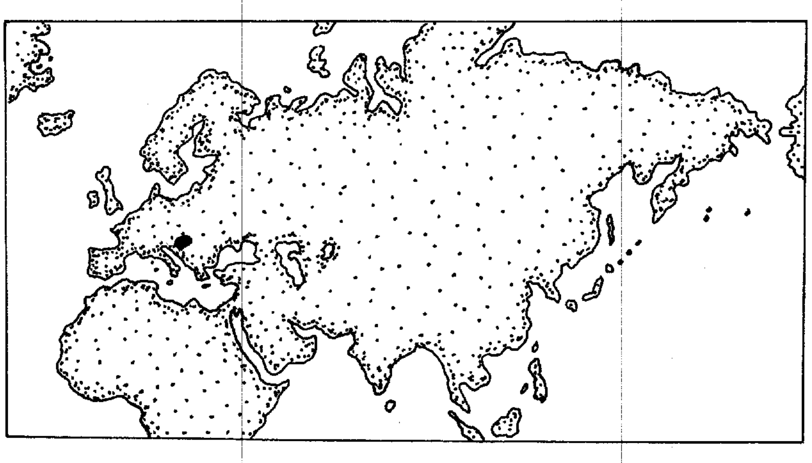
MAP 29 *A. shelichovii*



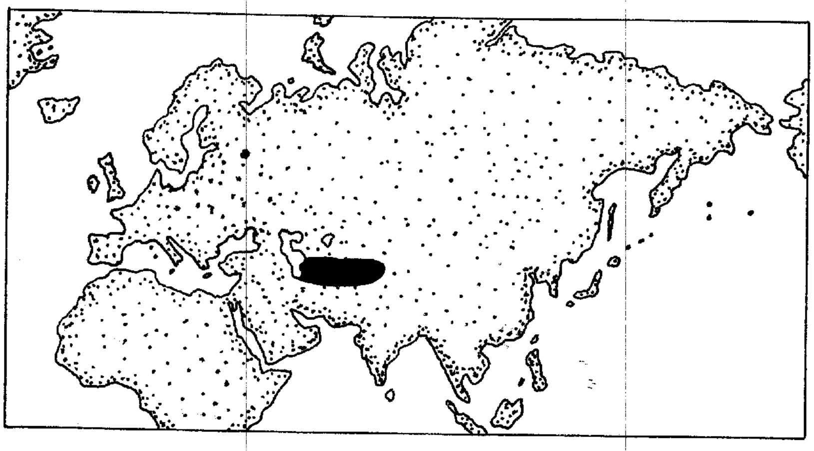
MAP 30 *A. campylorrhynchus*



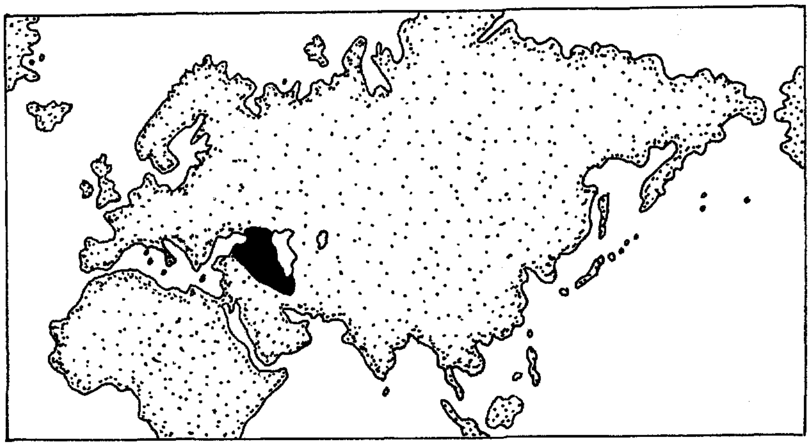
MAP 31 *A. interpositus*



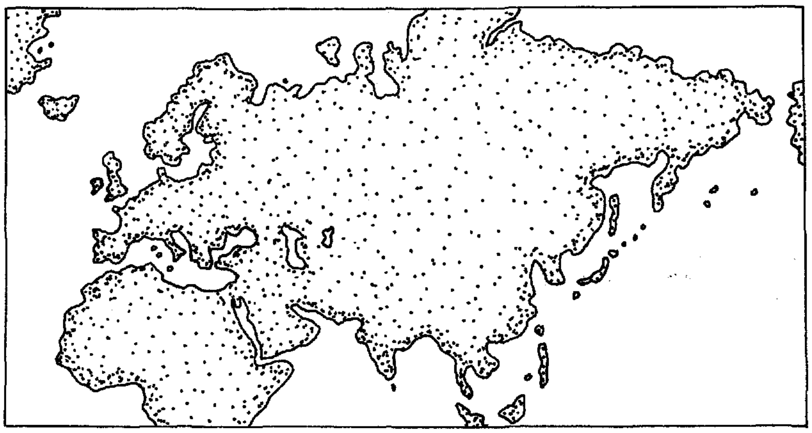
MAP 32 *A. peterfii*



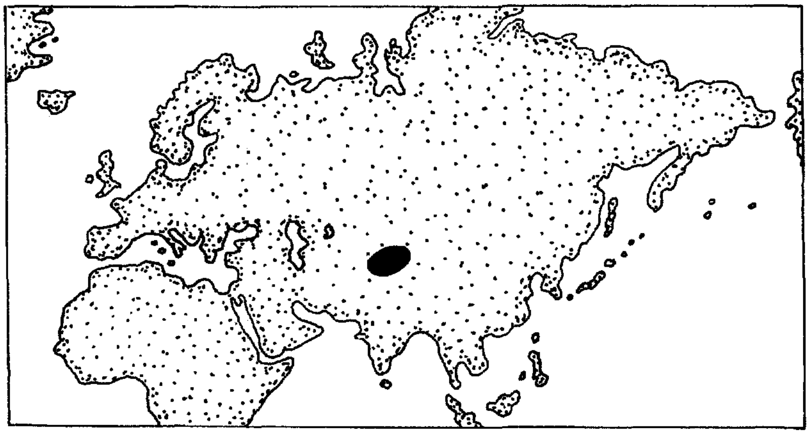
MAP 33 *A. suluklensis*



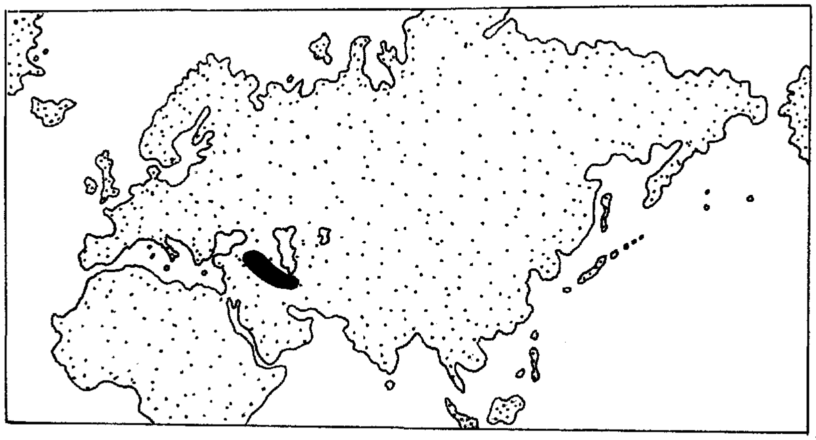
MAP 34 *A. lagurus*



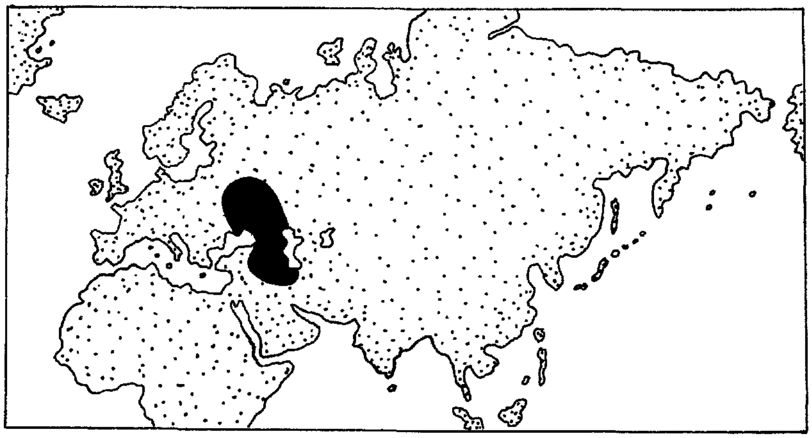
MAP 35 *A. andreji*



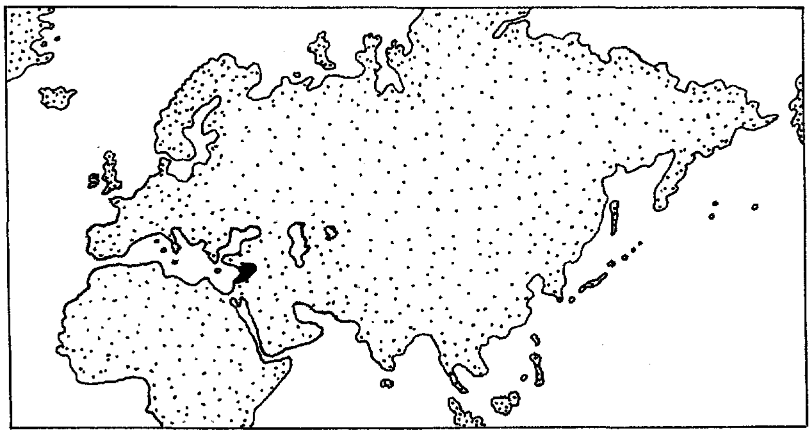
MAP 36 *A. aksuense*



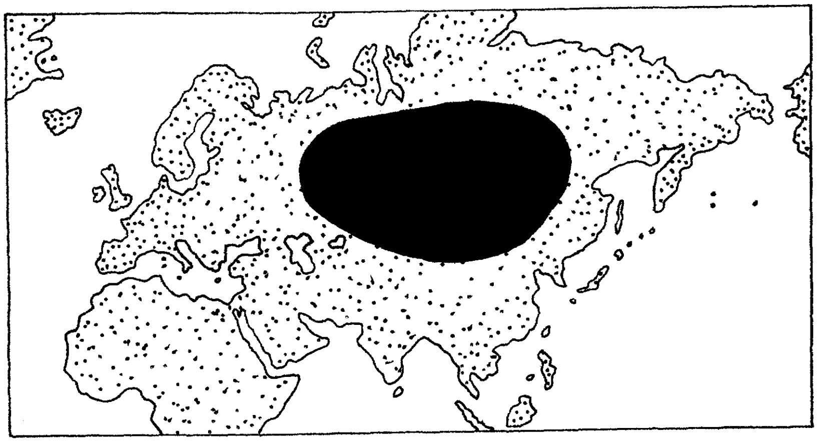
MAP 37 *A. macrourus*



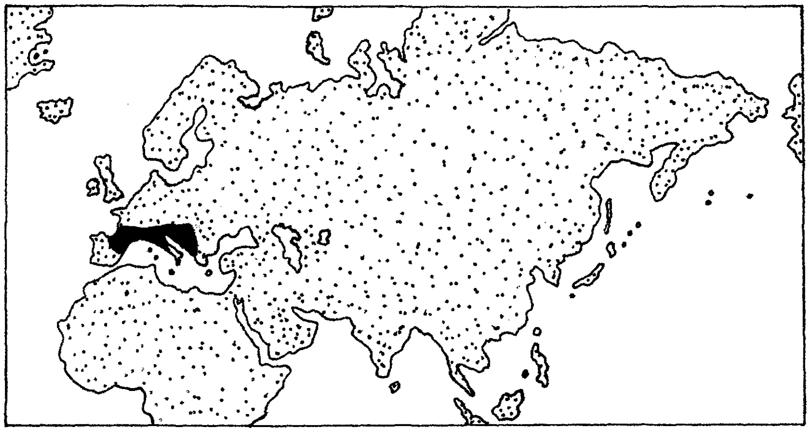
MAP 38 *A. ponticus*



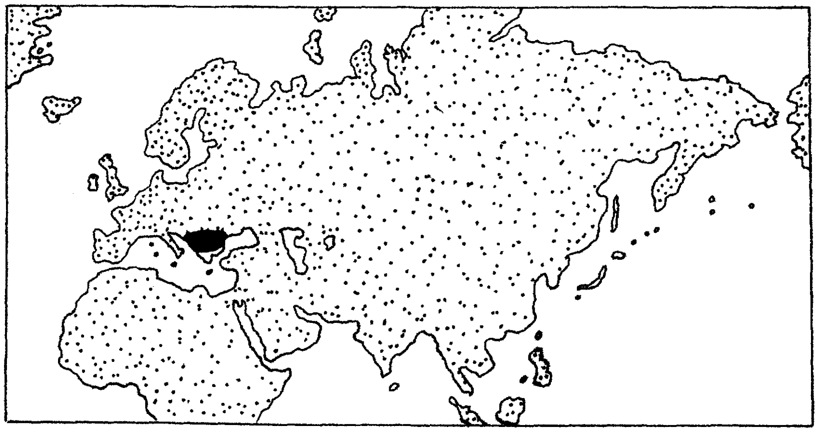
MAP 39 *A. expansus*



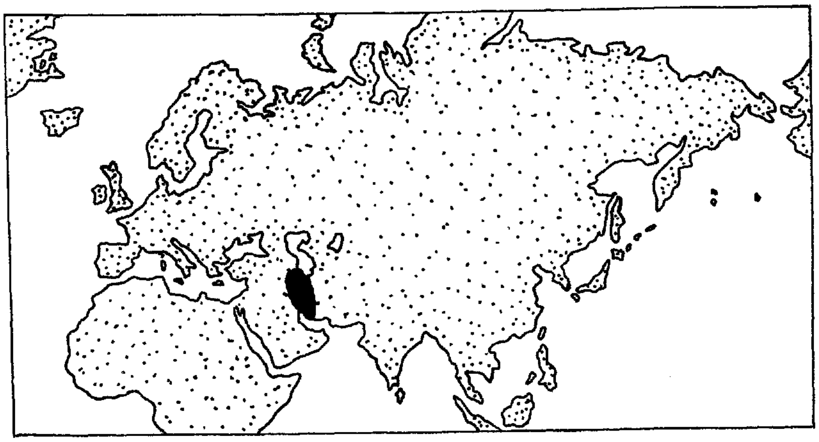
MAP 40 *A. mongholicus*



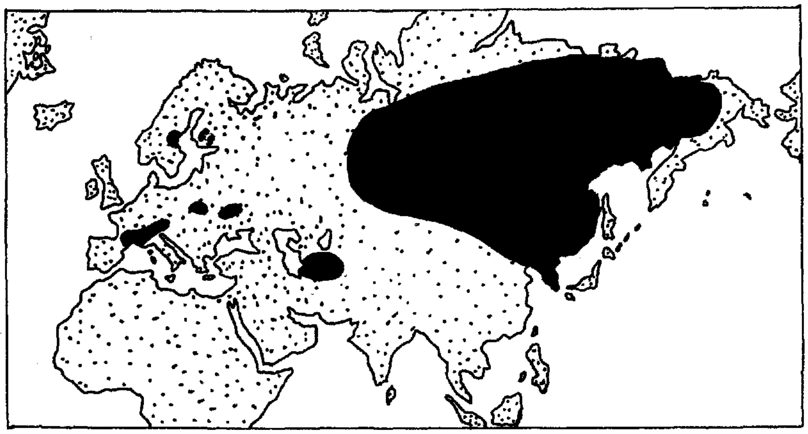
MAP 41 *A. purpureus*



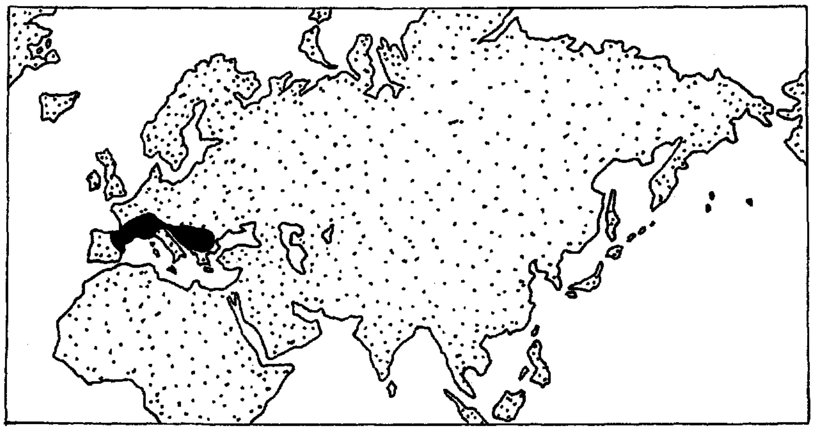
MAP 42 *A. illyricus*



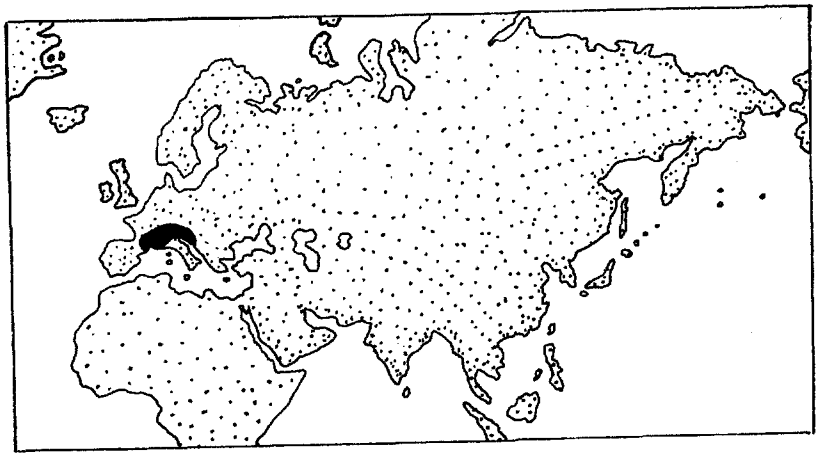
MAP 43 *A. verus*



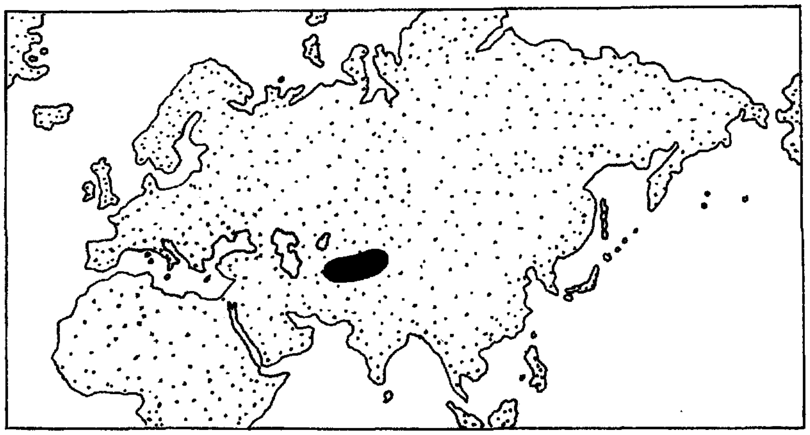
MAP 44 *A. penduliflorus*



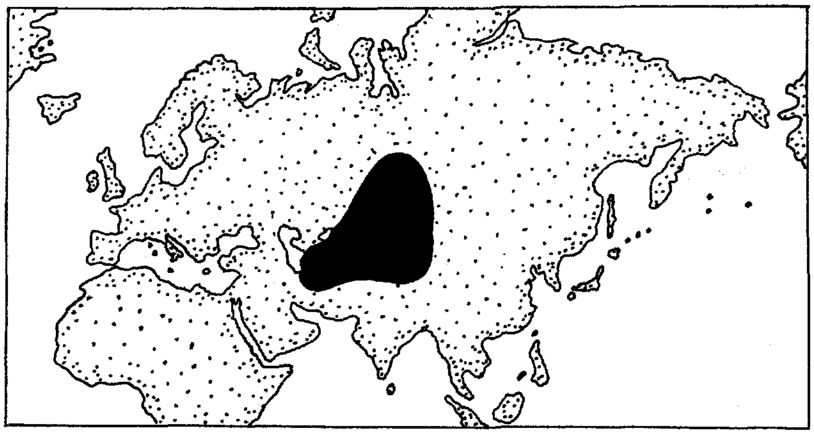
MAP 45 *A. sempervirens*



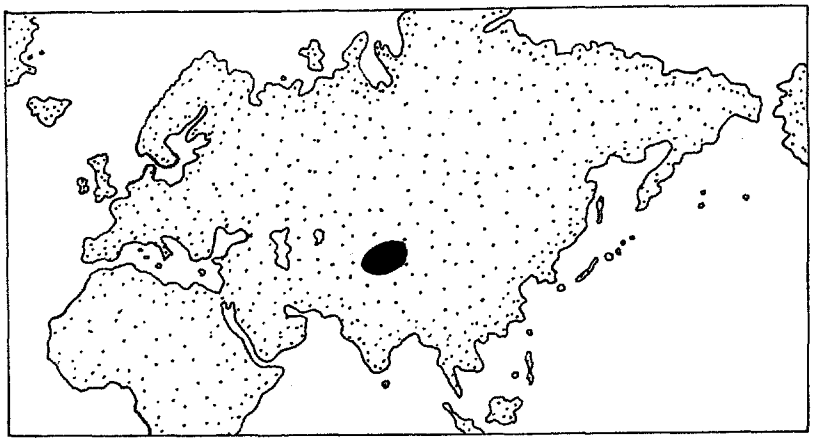
MAP 46 *A. leontinus*



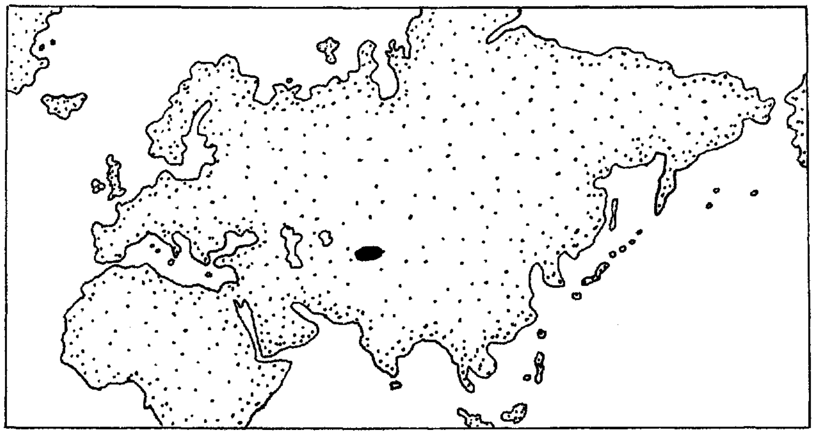
MAP 47 *A. coluteocarpus*



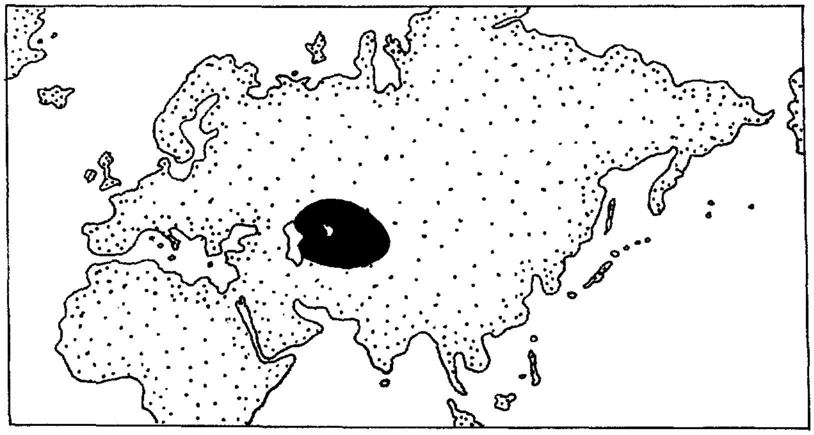
MAP 48 *A. tibetanus*



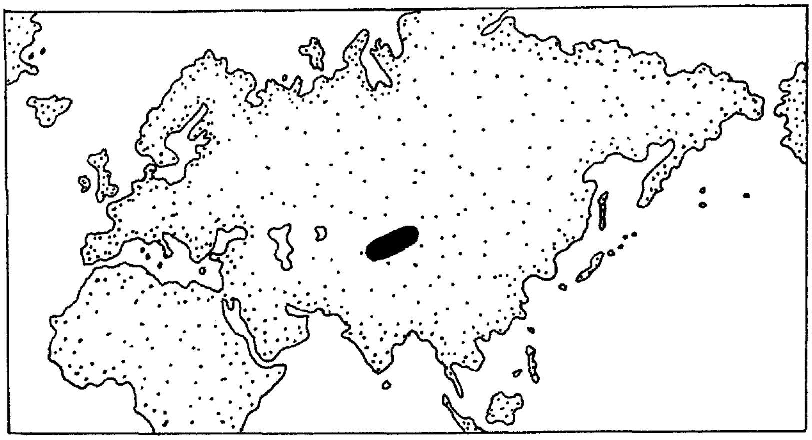
MAP 49 *A. stenanthus*



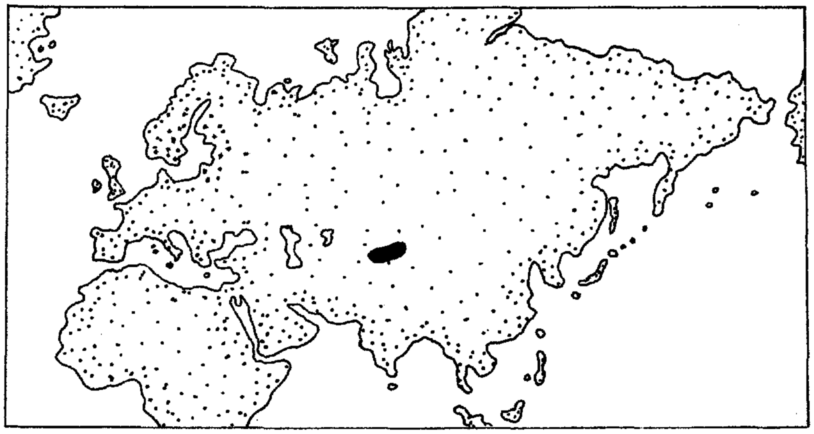
MAP 50 *A. eremospartoides*



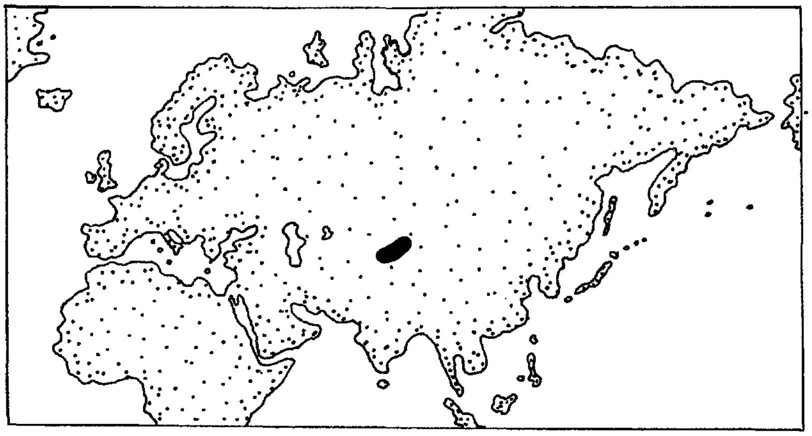
MAP 51 *A. schrenkianus*



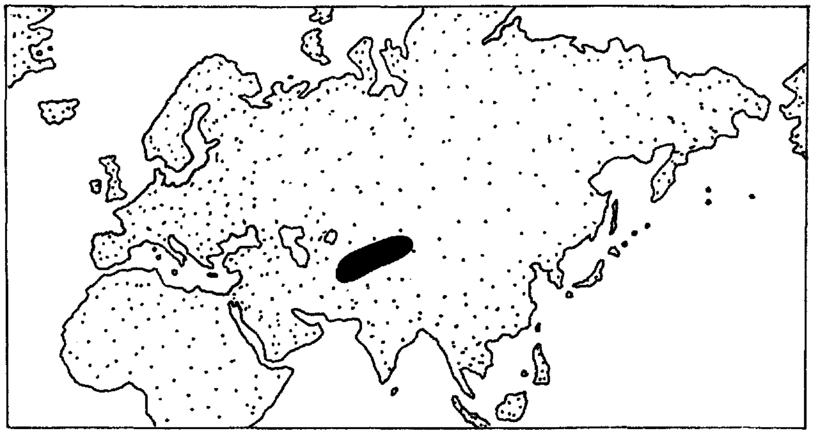
MAP 52 *A. platyphyllus*



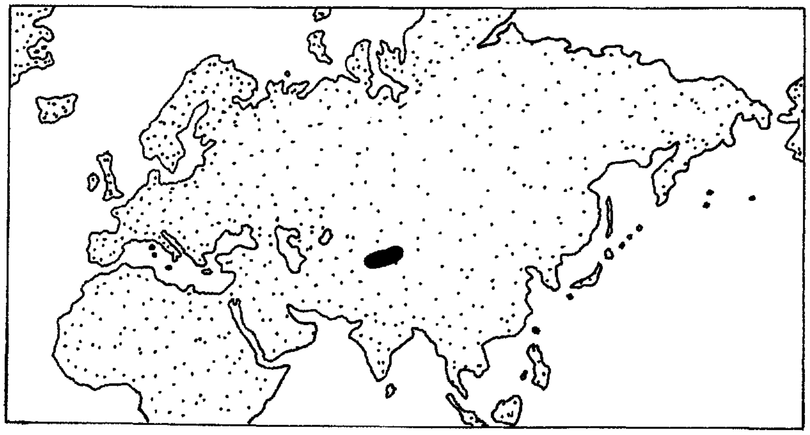
MAP 53 *A. nigrimontanus*



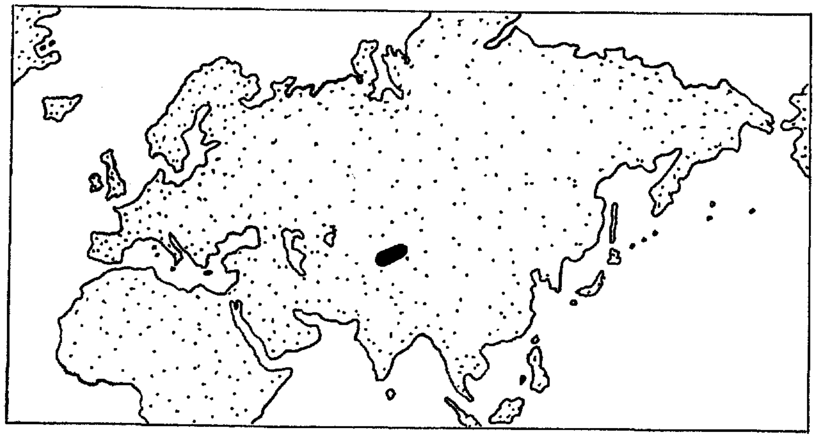
MAP 54 *A. macronyx*



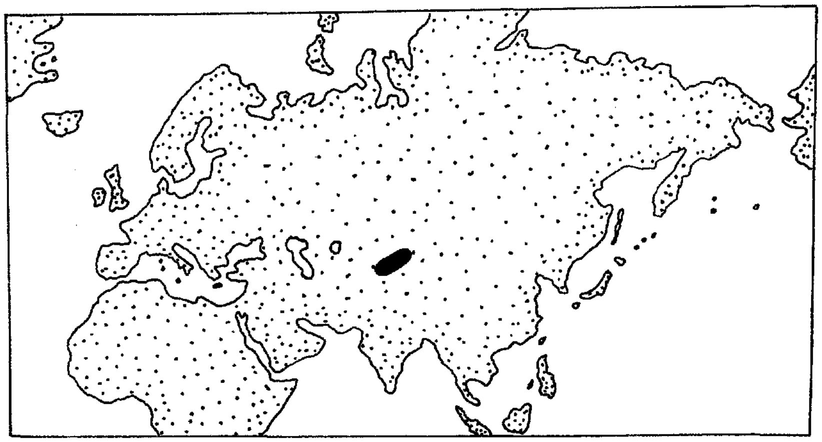
MAP 55 *A. lasiosemius*



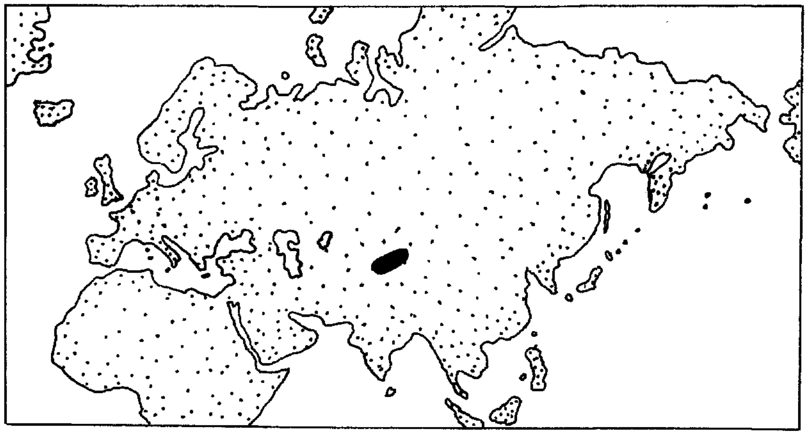
MAP 56 *A. skornjakovii*



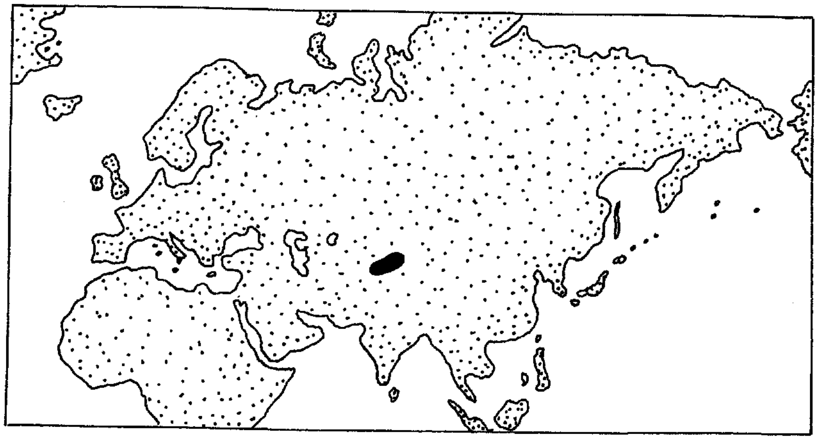
MAP 57 *A. hissaricus*



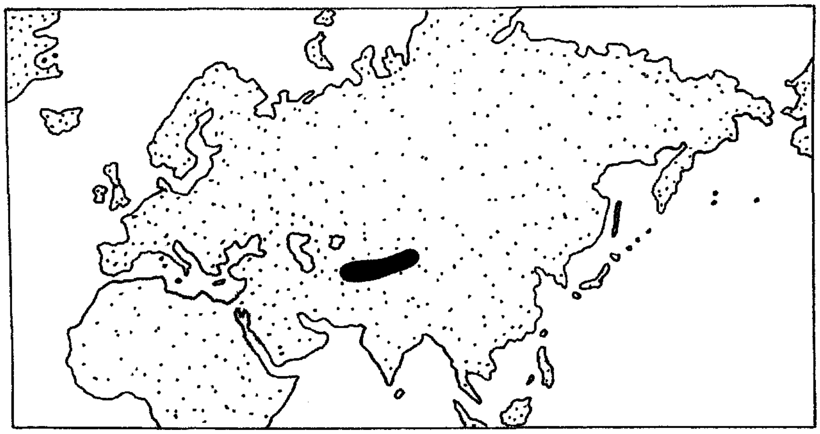
MAP 58 *A. eximius*



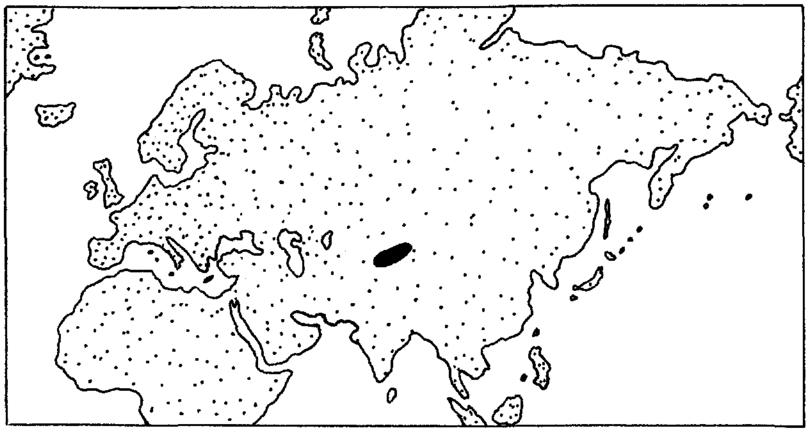
MAP 59 *A. iskanderi*



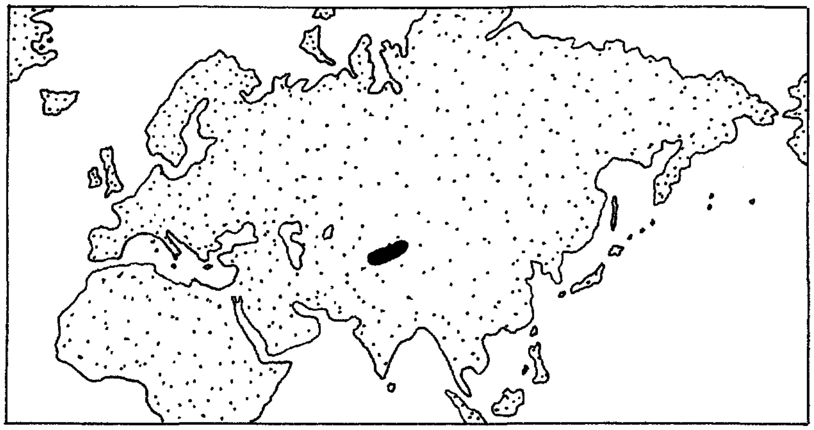
MAP 60 *A. turkestanus*



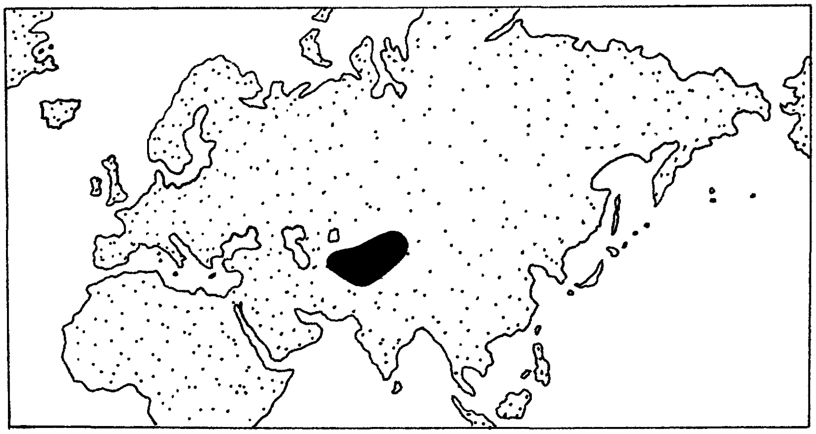
MAP 61 *A. kurdaicus*



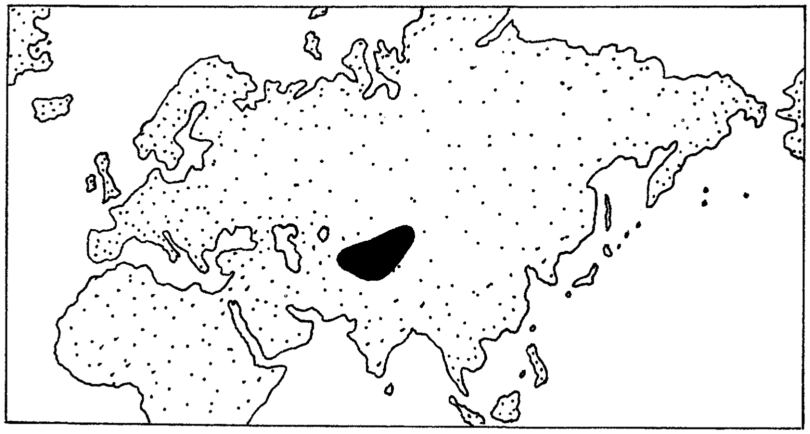
MAP 62 *A. uninodus*



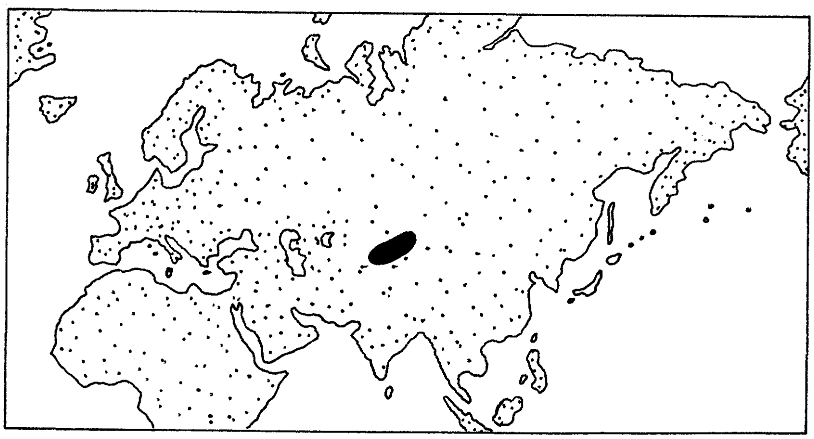
MAP 63 *A. cottenianus*



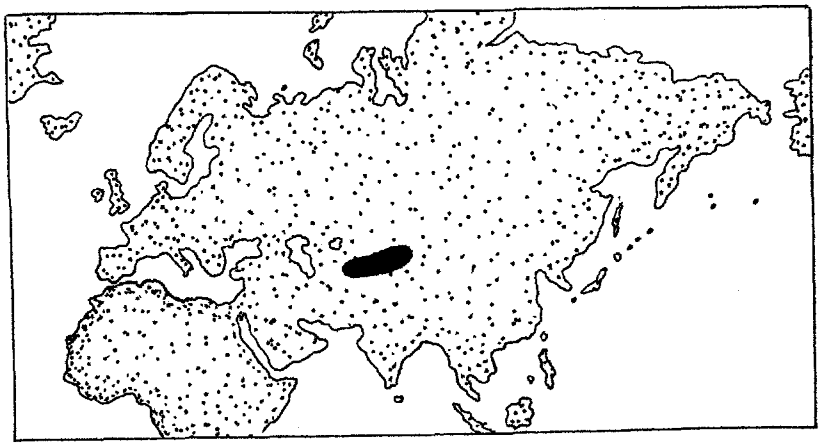
MAP 64 *A. sesamoides*



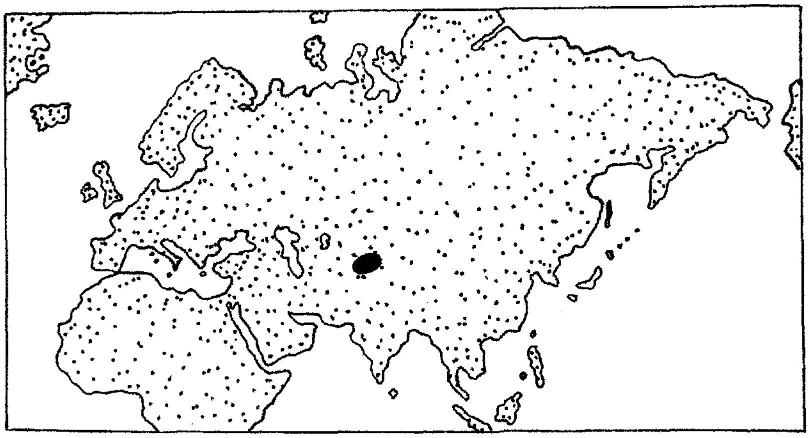
MAP 65 *A. globiceps*



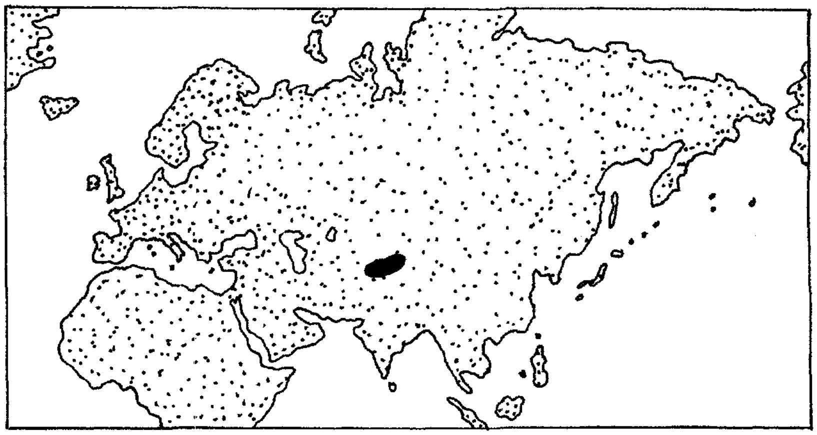
MAP 66 *A. ugamicus*



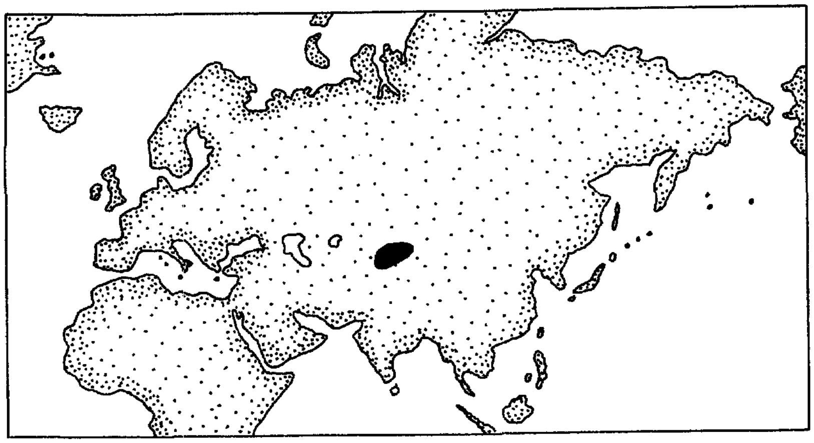
MAP 67 *A. bungei*



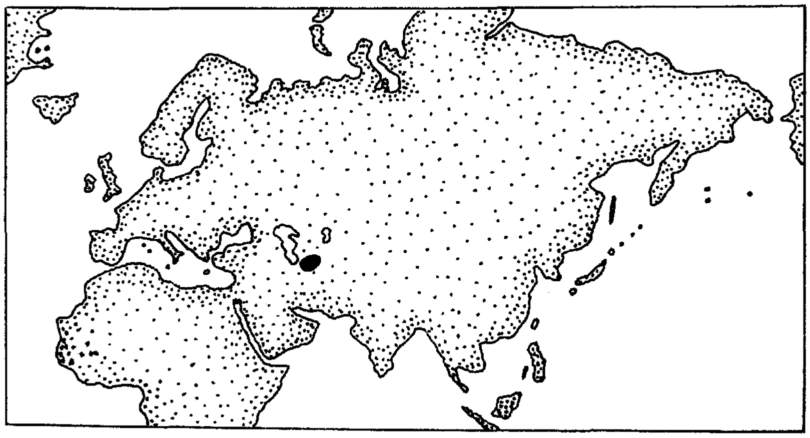
MAP 68 *A. xanthomeloides*



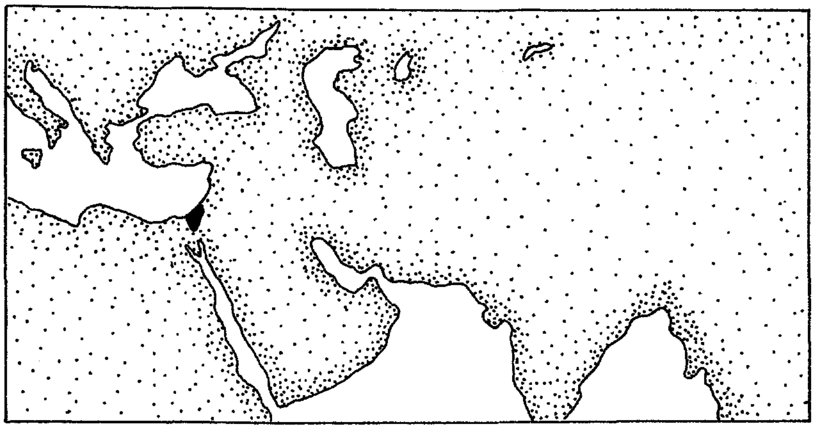
MAP 69 *A. lanuginosus*



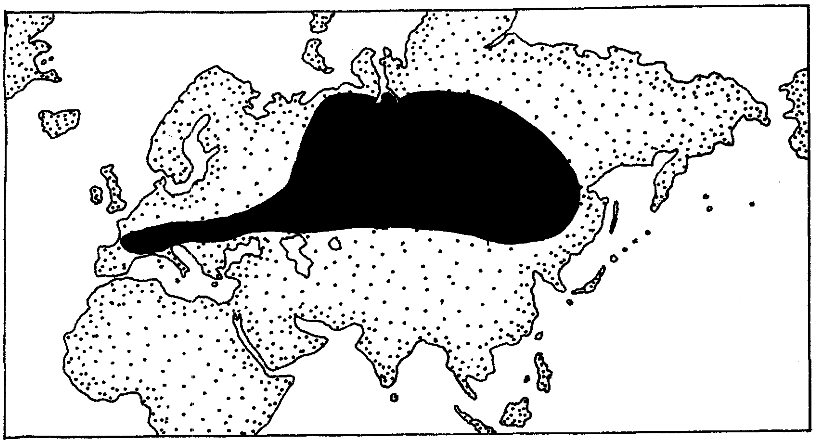
MAP 70 *A. xipholobus*



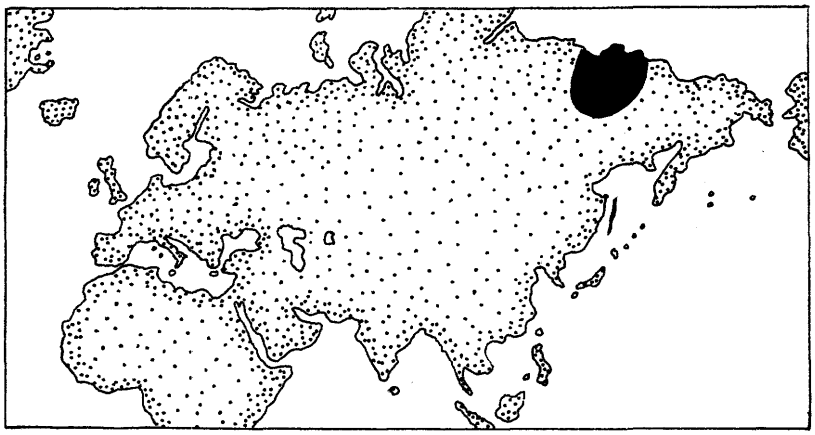
MAP 71 *A. litvinovii*



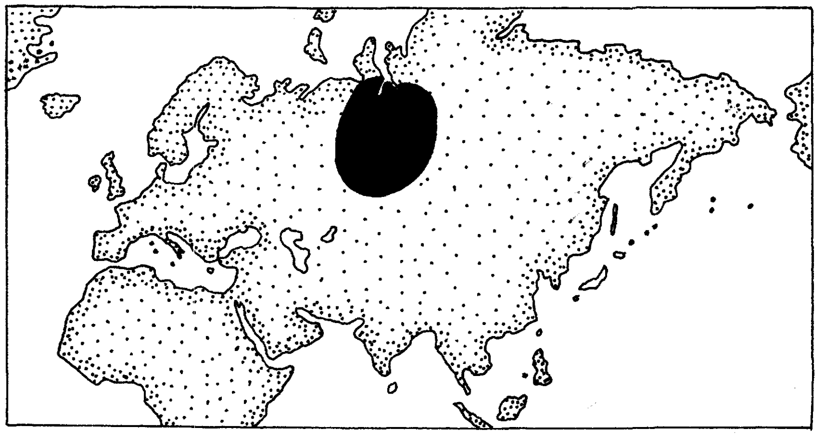
MAP 72 *A. amalecitanus*



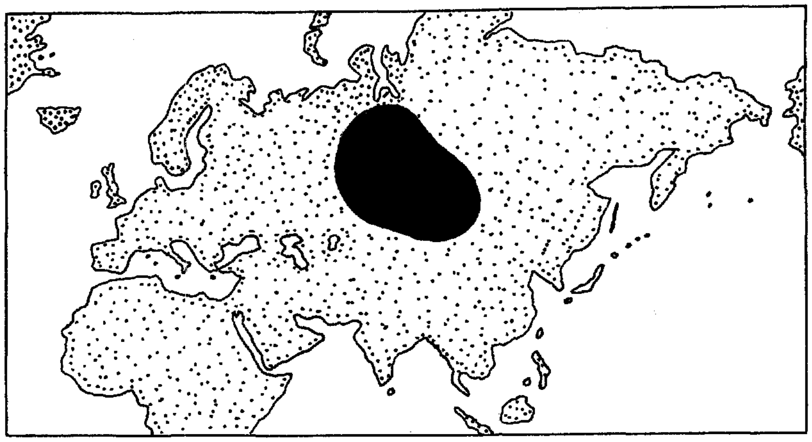
MAP 73 *A. tugarinovii*



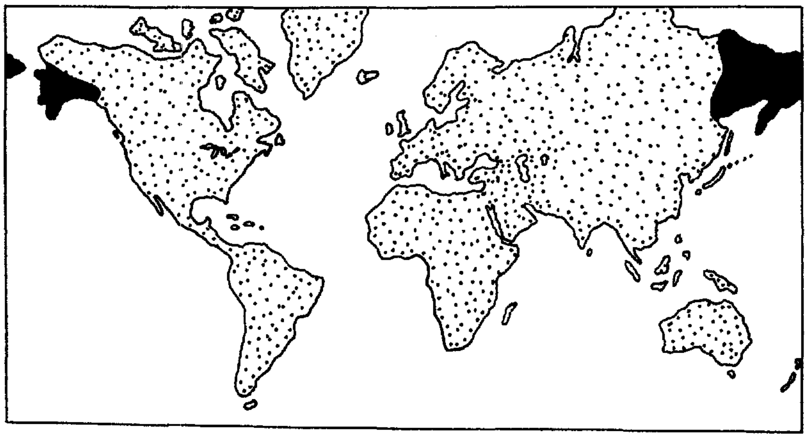
MAP 74 *A. richardsonii*



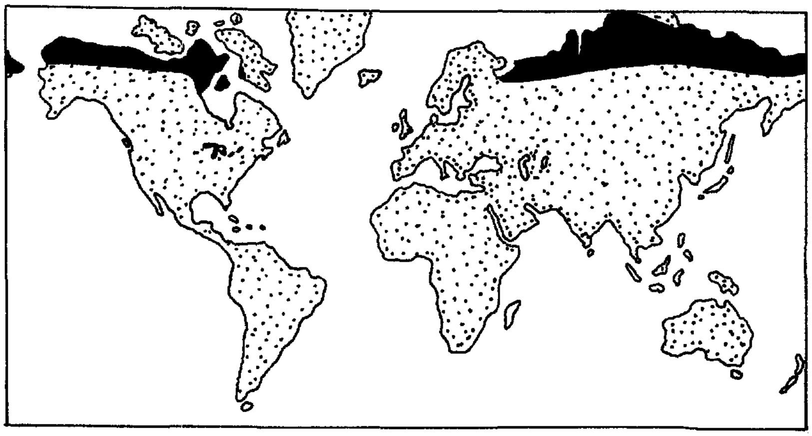
MAP 75 *O. argentea*



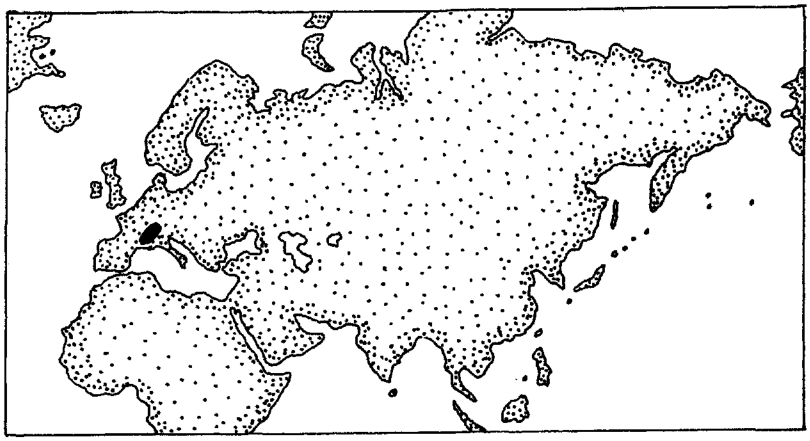
MAP 76 *O. sulphurea*



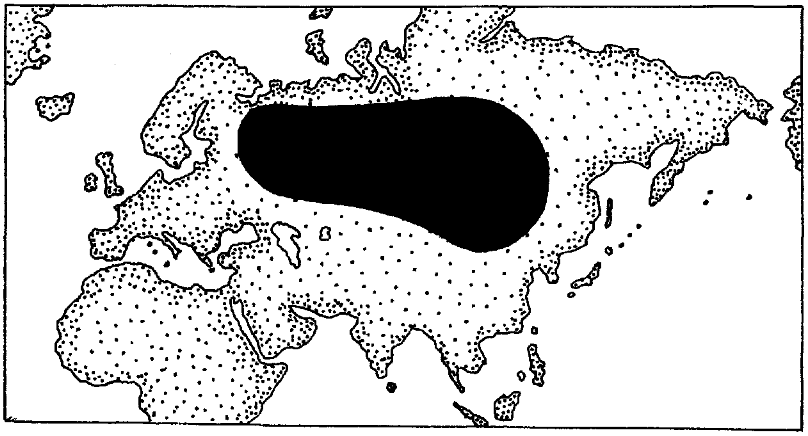
MAP 77 *O. mertensiana*



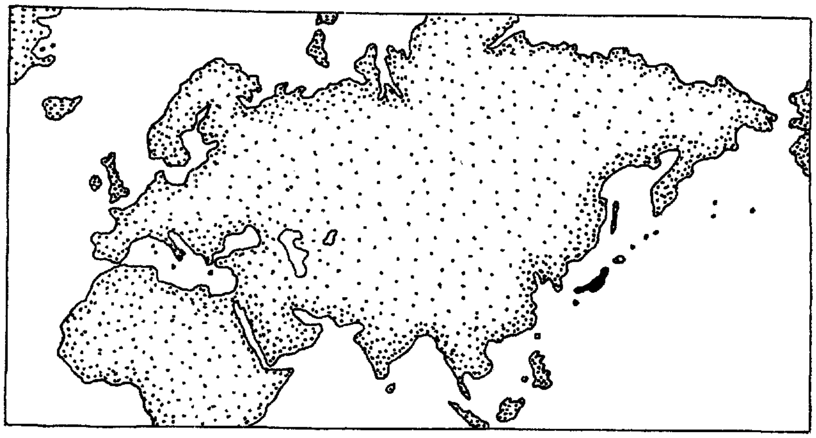
MAP 78 *O. arctica*



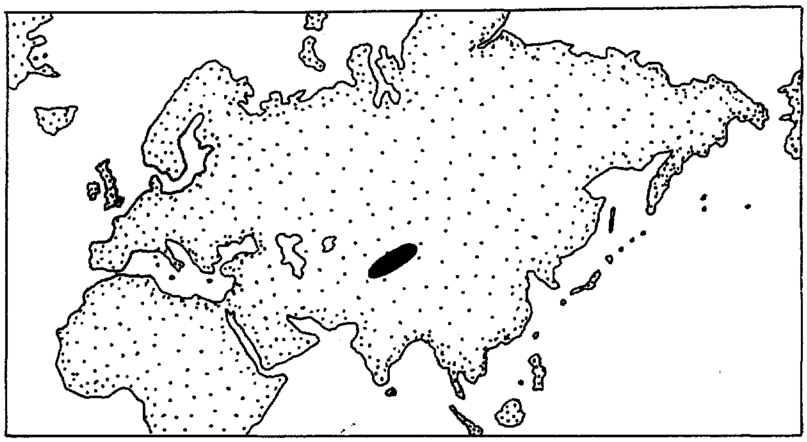
MAP 79 *O. foetida*



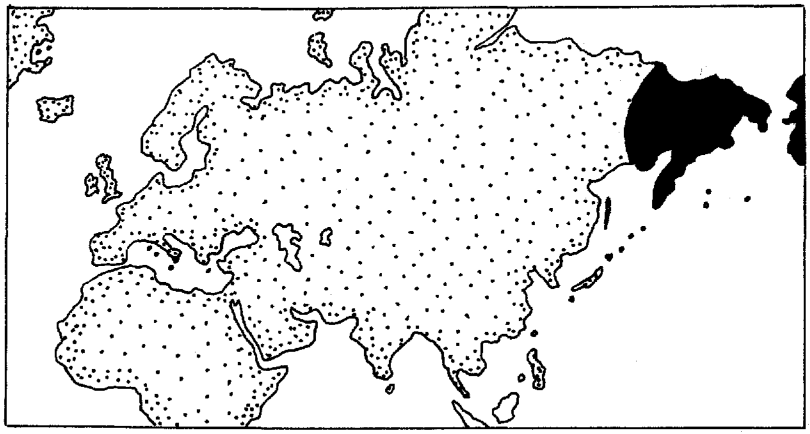
MAP 80 *O. uralensis*



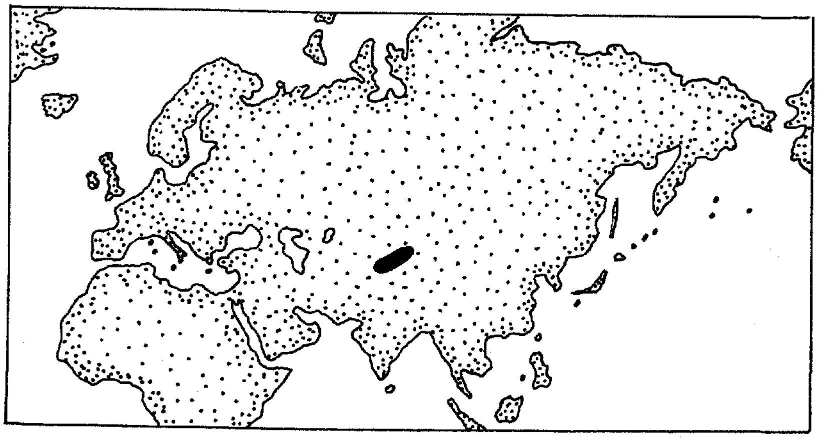
MAP 81 *O. japonica*



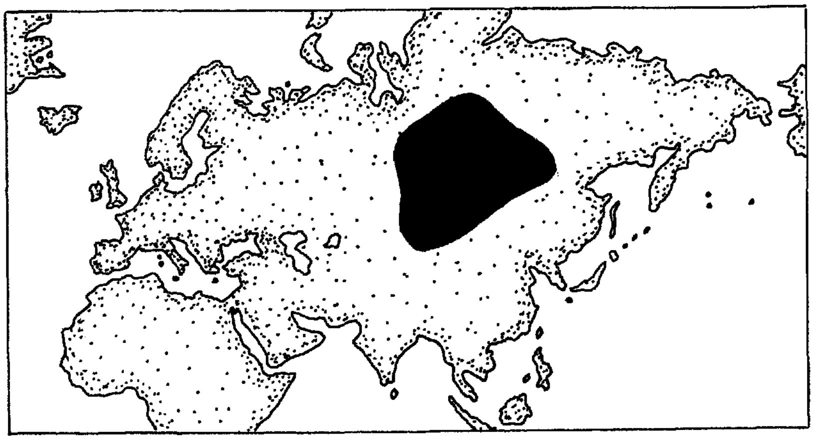
MAP 82 *O. trichocalycina*



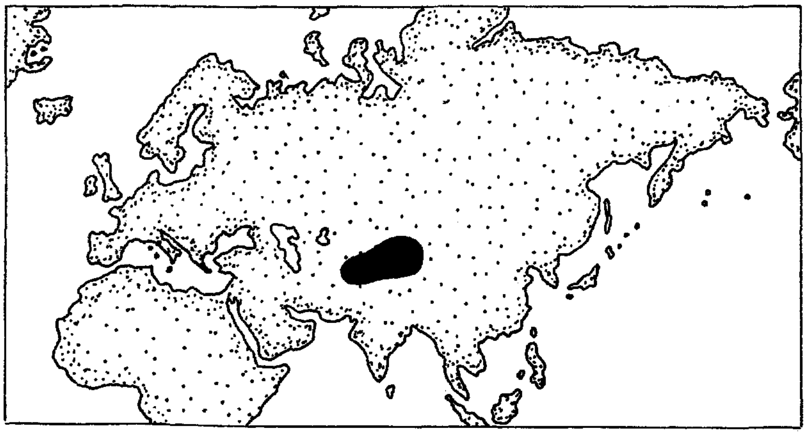
MAP 83 *O. nigrescens*



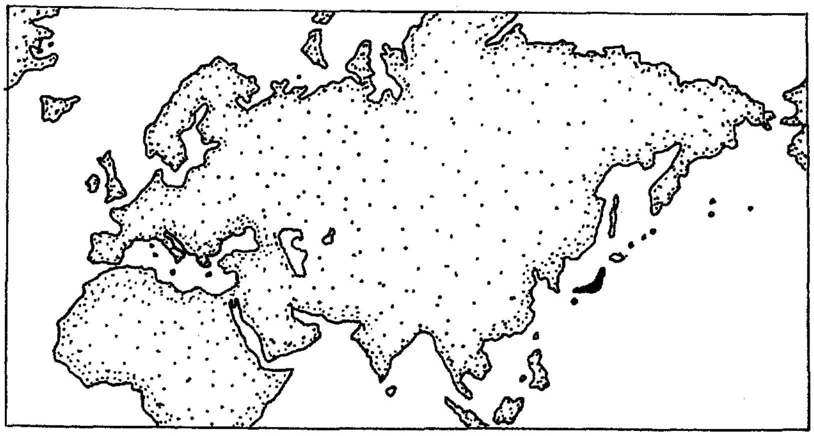
MAP 84 *O. karataviensis*



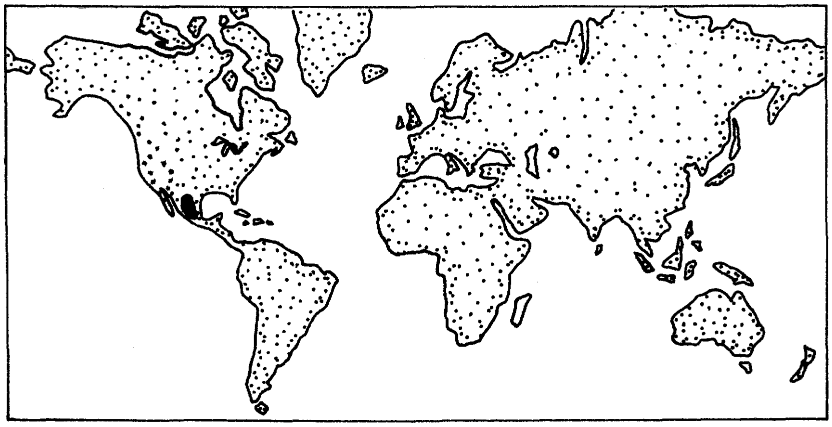
MAP 85 *O. schischkinii*



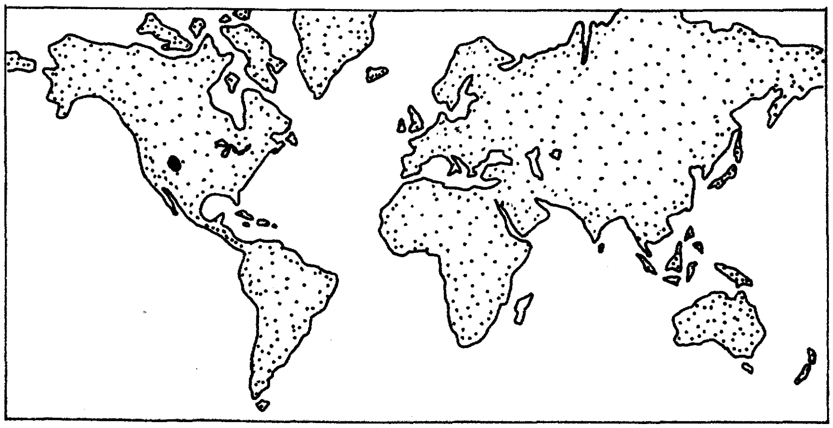
MAP 86 *O. chiliophylla*



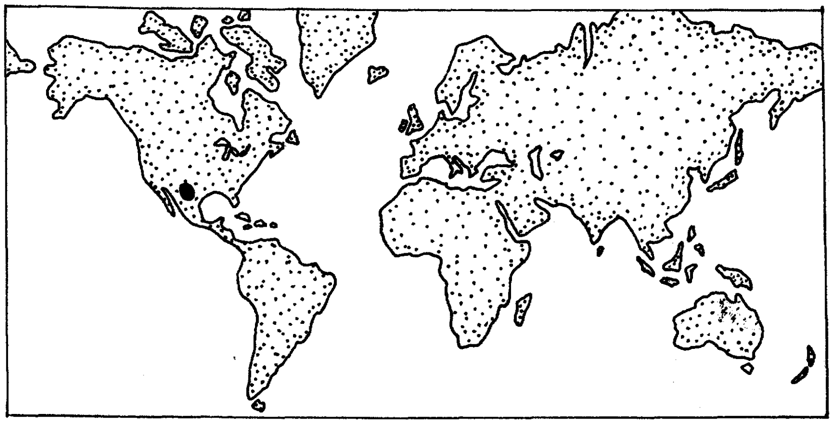
MAP 87 *O. megalantha*



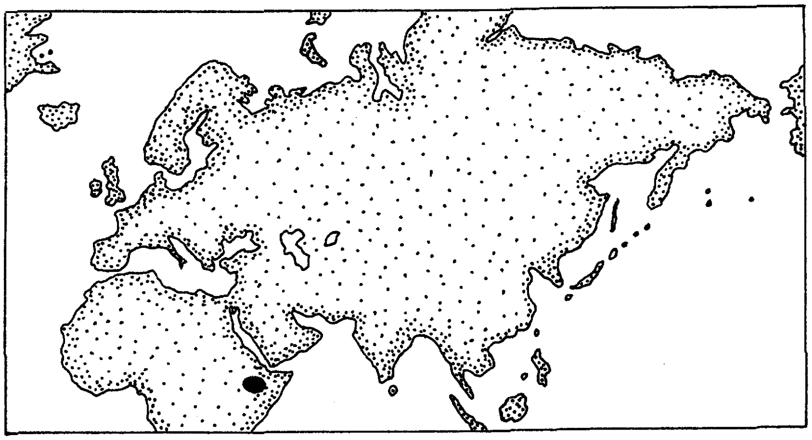
MAP 88 *A. hypoleucus*



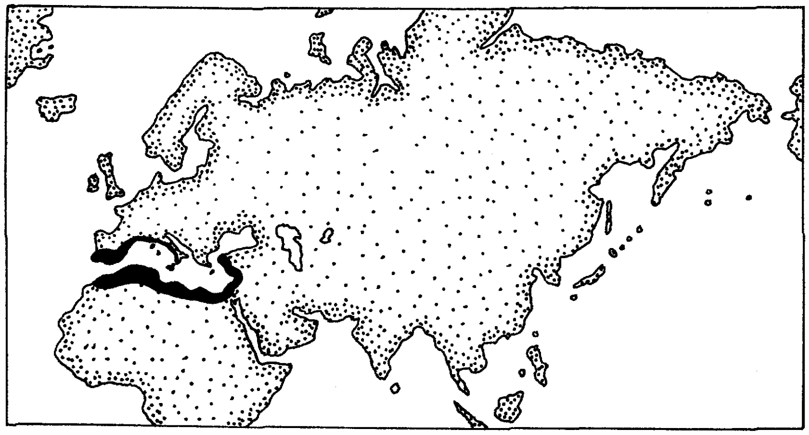
MAP 89 *A. sabulosus*



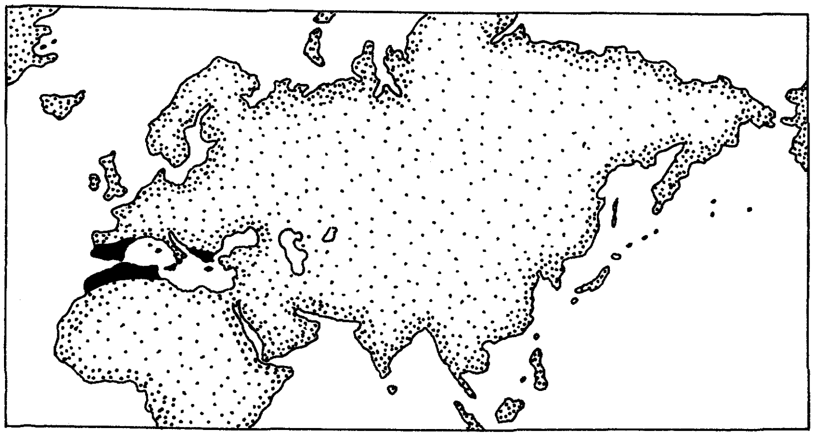
MAP 90 *A. terlinguensis*



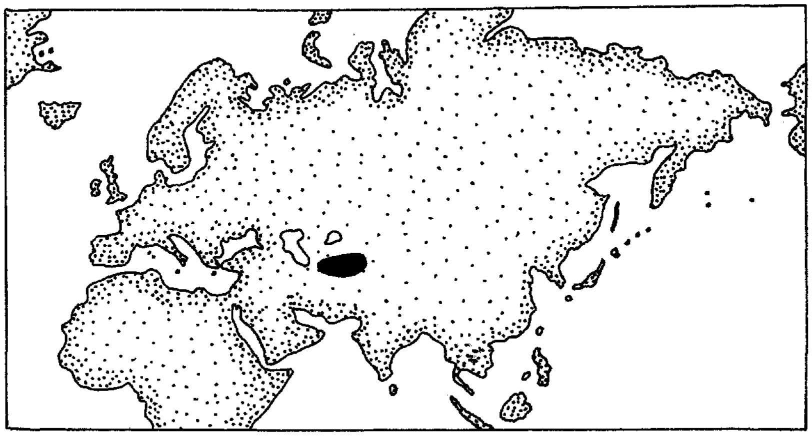
MAP 91 *A. somalensis*



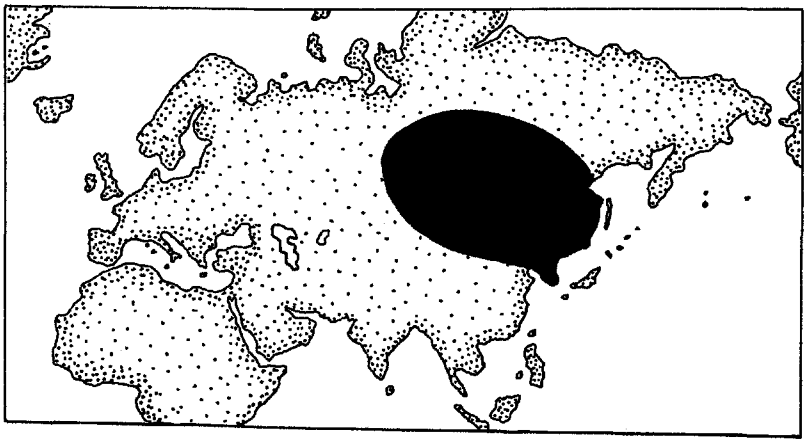
MAP 92 *A. boeticus*



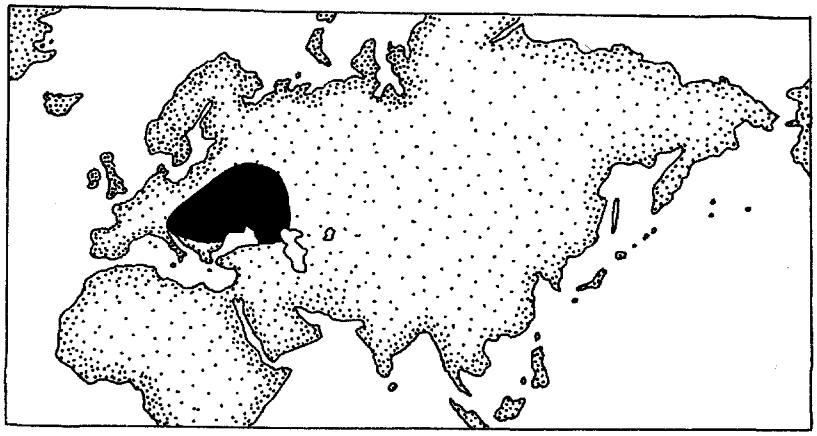
MAP 93 *A. pentaglottis*



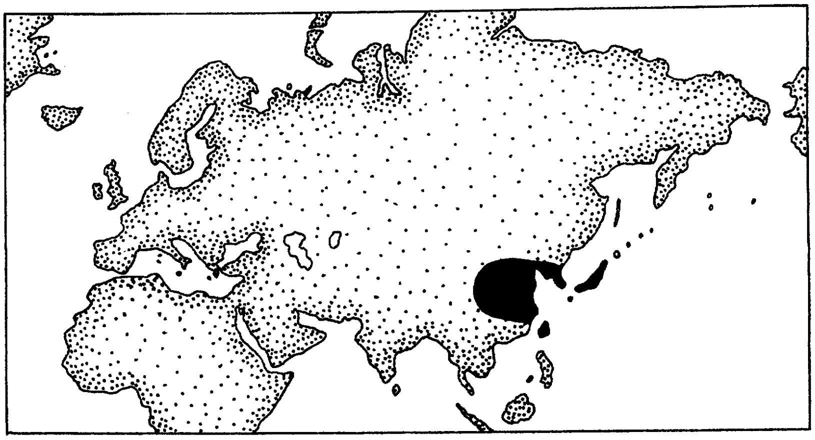
MAP 94 *A. schahrudensis*



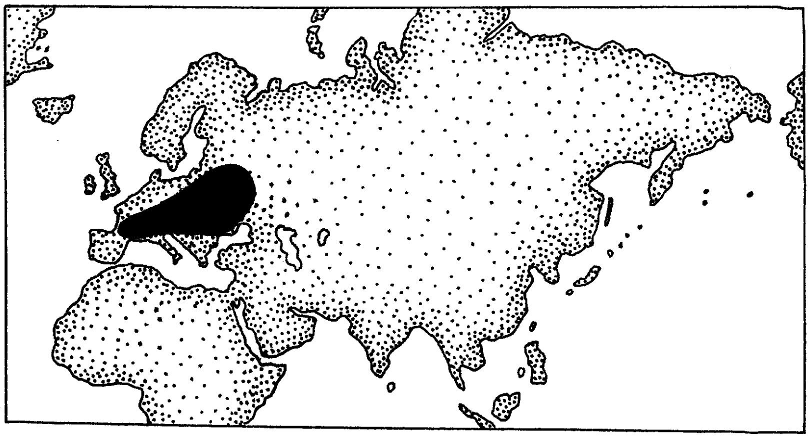
MAP 95 *A. membranaceous*



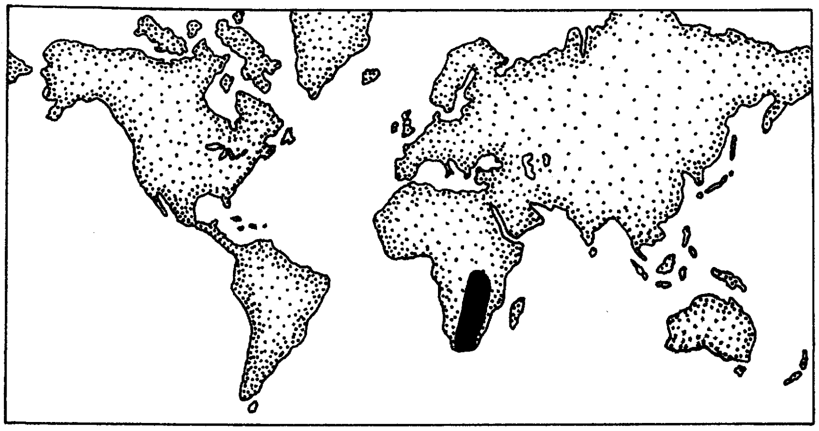
MAP 96 *A. asper*



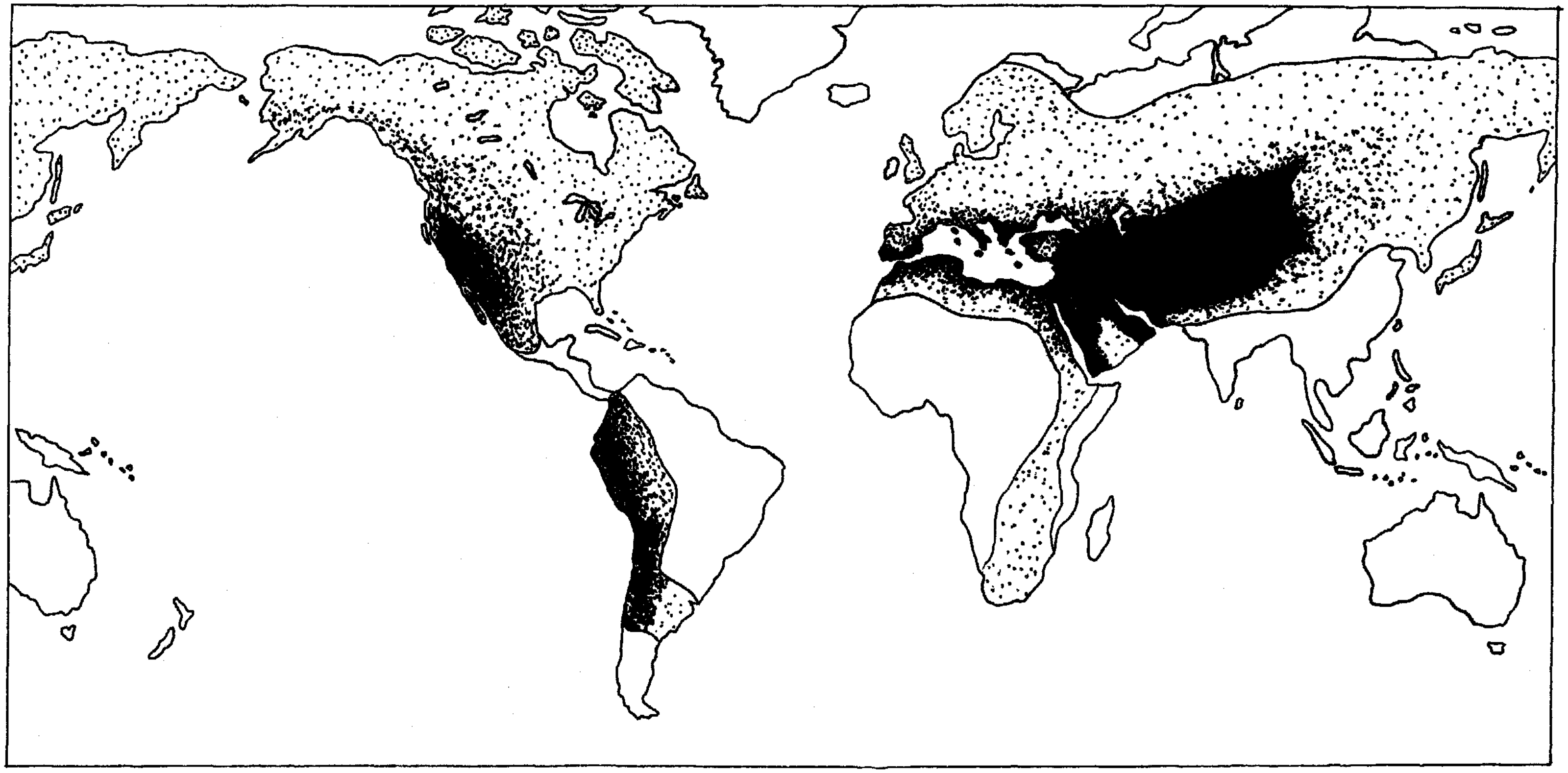
MAP 97 *A. sinicus*



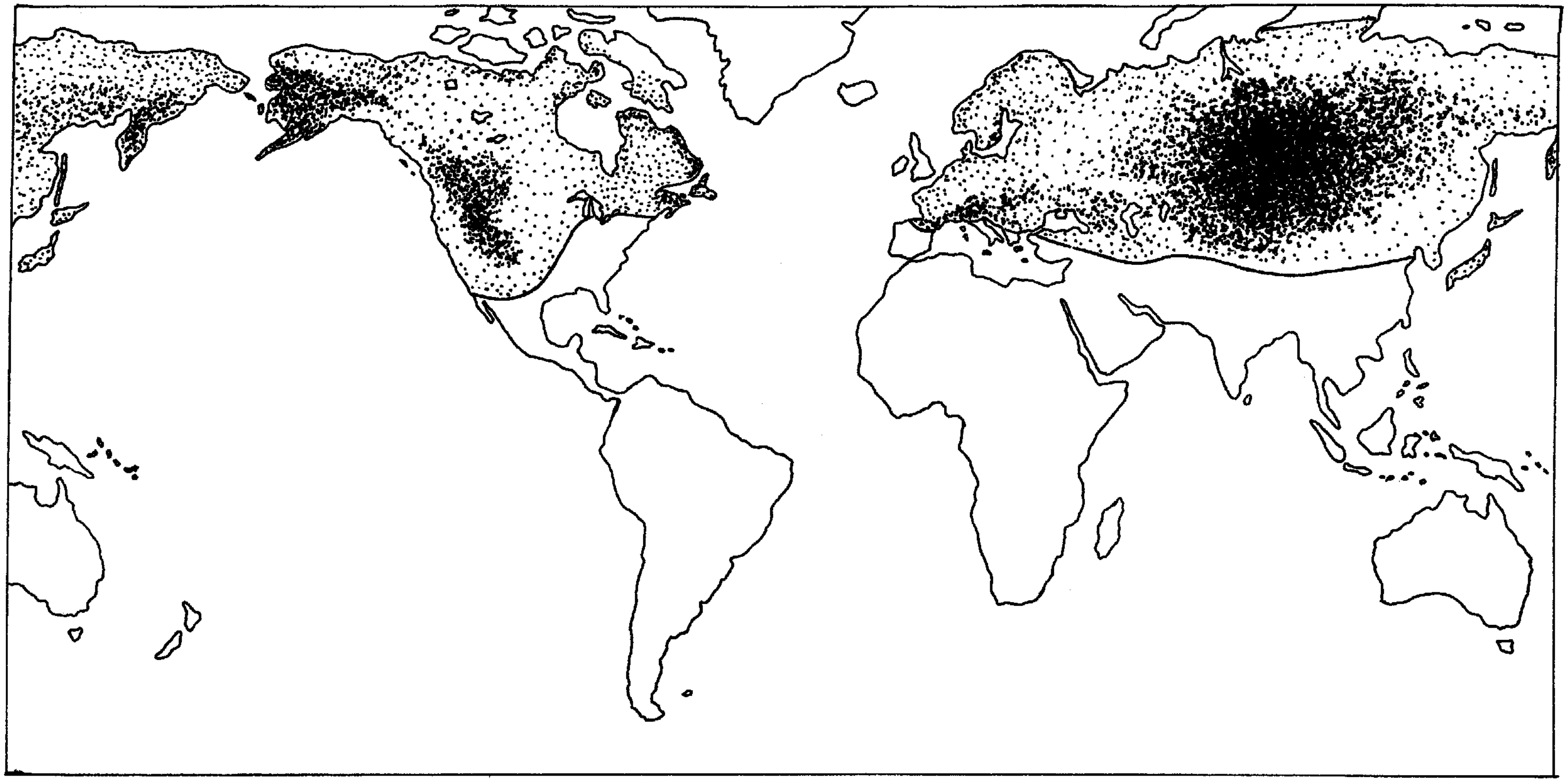
MAP 98 *A. exscapus*



MAP 99 *A. burkeanus*



MAP 100. Distribution of the genus *Astragalus*



MAP 101. Distribution of the genus *Oxytropis*

APPENDIX C

List of known chromosome counts in *Astragalus* and *Oxytropis*.

Species	Section	n	2n	Reference and Species Location
A. aboriginum Rich.	Onobrychium	8		Ledingham (57). Canada.
A. abyssinicus (Hochst.) Rich.	Diplotheca		16	Ledingham (60). Kenya.
= *A. burkeanus* Benth.			16	Rever (61).
A. acinaciferus Boiss.	Chronopus		16	Frahm-Leliveld (57). Israel.
A. ackerbergensis Freyn.	Proselius		32	Rever (61). U.S.S.R.
A. adsurgens Pall.	Onobrychium		32	Sakai (35). Japan.
A. aksuensis Bge.	Cenanthrum		16	Rever (61). U.S.S.R.
A. alexandrinus Boiss.	Myobroma		16	Rever (61). Egypt.
A. allochrous Gray	Inflati		22	Head (57). U.S.A.
A. alopecias Pall.	Alopecias		16	Rever (61). U.S.S.R.
A. alopecuroides L.	Alopecias	8		Kreuter (30). Europe.
= *A. alopecurus* Pall.			16	Ledingham (60). U.S.S.R.
A. alpinus L.	Onobrychium		16,32 16,32	Favarger (49). Europe. Ledingham (60). Canada.
A. altaicus Bunge	Myobroma		16	Tschechow (30). U.S.S.R.
A. amalecitanus Boiss.	Ammodendron		16	Rever (61). Israel.
A. americanus (Hook). Jones	Cenanthrum	8		Ledingham (58). Canada
= *A. frigida americana*				
A. andersonii Gray	Hamosi		24	Head (57). U.S.A.
A. andreji Rzazade			16	Rever (61). U.S.S.R.
A. aristatus L'Herit.	Tragacanthae		16	Tschechow (35). Europe.
A. arrectus Gray	Reventi-Arrecti		24	Head (57). U.S.A.
A. arthurii Jones	Hamosi		24	Head (57). U.S.A.

Species	Section	n	2n	Reference and Species Location
A. asper Jacq.	Pedina	24		Tschechow (35). U.S.S.R.
			48	Rever (61). U.S.S.R.
A. beathii	Preussiani	12		Vilkomerson (43). U.S.A.
A. Beckwithii T. & G. var. weiserensis Jones	Inflati		22	Head (57). U.S.A.
A. bergii Hieronymus			26	Ledingham (60). Argentina.
A. bisulcatus (Hook.) Gray	Bisulcati	12 12		Vilkomerson (43). U.S.A. Ledingham (57). Canada.
A. boeticus L.	Cyamodes	8	 30 30 30	Kreuter (29,30) Tschechow (35) Med. region Ledingham (60 Rever (61)
A. bolanderi Gray	Reventi-Arrecti	11		Snow (59). U. S. A.
A. bombycinus Boiss.	Platyglottis		16	Rever (61). Iraq, Egypt
A. brachylobus DC.	Xiphidium	48		Tschechow (35). U.S.S.R. Tischler (38)
A. brachypetalus Trautv.	Stereothrix		16	Rever (61). U.S.S.R.
A. brazoensis Buckley	Didymocarpi		22	Turner and Fearing (59). U.S.A Ledingham (60). U.S.A.
A. brevidens Freyn et Sint.	Onobrychium		64	Ledingham (60). U.S.S.R.
A. bubaloceras Maire		14-15 16		Senn (38). Morocco Tschechow (35).
A. buceras Willd.		8		Tischler (38).
A. bungei C. Winkl. & Fedtsch.	Platyglottis		32	Rever (61). U.S.S.R.
A. burkeanus Benth. = A. abyssinicus (Hochst.) Rich.			16	Ledingham (60). Kenya Rever (61).
A. campylorrhynchus Fisch. et Mey.	Harpilobus	18	 16	Tschechow (35). U.S.S.R. Rever (61). U.S.S.R.

Species	Section	n	2n	Reference and Species Location
A. campylotrichus Bge.	Campylotrichon	16		Tschechow (35).
			16	Rever (61). U.S.S.R.
A. canadensis L.	Uliginosi	8		Vilkomerson (43). U.S.A.
		8		Ledingham (57).
			16	Head (57). U.S.A.
			16	Ledingham (60).
A. candidissimus Led.	Leucophysa		16	Tschechow (30). U.S.S.R.
A. canonis Jones	Podo-Sclerocarpi	11		Vilkomerson. U.S.A.
A. carinatus (H. & A.) Reiche			26	Ledingham (60). Argentina
A. casei Gray	Podo-Sclerocarpi	11		Vilkomerson. U.S.A.
A. chamaeleuce Gray	Argophylli		22	Head (57). U.S.A.
A. chinensis L.	Nuculiella	8		Tschechow (35). China.
			16	Ledingham (60).
A. chlorostachys Lindl.			16	Ledingham (60). India
			16	Rever (61). India.
A. cibarius Sheld.	Argophylli		22	Head (57). U.S.A.
A. cicer L.	Eu-Hypoglottis		64	Tschechow (35). U.S.S.R.
			64	Ledingham (60). Europe.
A. collinus (Dougl. ex (Hook.) G. Don.	Collini			
var. collinus			24	Head (57). U.S.A.
var. laurentii (Rydh.) Barneby			24	Head (57). U.S.A.
A. coluteocarpus Boiss.	Coluteocarpus		16	Rever (61). U.S.S.R.
A. confertiflorus Gray	Ocreati	12		Vilkomerson (43). U.S.A.
			24	Ledingham (60). U.S.A.
A. congdonii Watson	Hamosi		26	Head (57). U.S.A.
A. conjunctus S. Wats	Reventi-Arrecti		24	Head (57). U.S.A.
A. contortuplicatus L.	Cycloglottis	8		Tischler (38). U.S.S.R.

Species	Section	n	2n	Reference and Species Locatio
A. cooperi Gray	Uliginosi		22	Ledingham (60). Canada.
A. corrugatus Bert.	Harpilobus		32	Rever (61). Iraq.
A. cottenianus Aitch. & Baker	Proselius		16	Rever (61). U.S.S.R.
A. crassicarpus Nutt.	Sarcocarpi	11 11	 22	Vilkomerson (43). U.S.A. Ledingham (58). Canada Ledingham (60). U.S.A.
A. cremospartioides		8		Tischler (38)
A. crotalariae Benth.	Inflati	12		Snow (59). U.S.A.
A. cruciatus Link. ssp. garamantum Maire	Oxyglottis	8		Quezel (55). N. Africa.
A. crukshanksii (H. & A.) Grisebach			26	Ledingham (60). Argentina.
A. cusickii Gray	Inflati		22	Head (57). U.S.A.
A. cylindraceus DC		8		Tischler (38). Armenia.
A. cymbaecarpus Brot.		8		Tischler (38).
A. danicus Retz.	Eu-Hypoglot-tis	8		Tischler (38). U.S.S.R.
A. darumbium (Bertero) Clos			22	Ledingham (60). Argentina.
A. dasyanthus Pall.	Erionotus	8		Tischler (38). U.S.S.R.
A. dauricus = A. dahuricus (Pall.) DC	Heterodontus			Tischler (38). Dahuria, China
A. desamus		8		Kreuter (28).
A. diaphanus Dougl. ex Hook.	Inflati		28	Head (57). U.S.A.
A. didymocarpus H. & A. Bot.	Didymocarpi		24	James (51). U. S. A.
A. dispermus Gray	Didymocarpi		26	James (51). U.S.A.
A. distinens Macloskie			26	Ledingham (60). Argentina.

Species	Section	n	2n	Reference and Species Location
A. distortus T & G.	Hamosi	13		Turner and Fearing (59). U.S.A.
			26	Ledingham (60). U.S.A.
A. drummondii Hooker	Galegiformes	11		Vilkomerson (43). U.S.A.
		11		Ledingham (57). Canada.
A. echinus DC.	Tragancantha		64	Tschechow (30). Near East.
A. edulis Dur.	Trimeniaeus	14?		Kreuter (30). Algeria
A. eremiticus Sheld. var. malheurensis (Heller) Barneby	Argophtlli		24	Head (57). U.S.A.
A. eremospartoides Rgl.	Corethrum		16	Rever (61). U.S.S.R.
A. eucosmus Robins	Malacothryx	16		Ledingham (57). Canada.
			32	Ledingham (60). Canada.
A. eximius Bge.	Alopecias		16	Rever (61). U.S.S.R.
A. expansus Boiss.			16	Rever (61). U.S.S.R.
A. exscapus L.	Myobroma		16	Tschechow (30). U.S.S.R.
			16	Ledingham (60). Spain
			16	Rever (61). Switzerland.
A. falcatus Lam.	Euodmus	8		Kreuter (29,30).
			16	Ledingham (60). Europe.
A. falciformis Derf.			16	Ledingham (60). Spain.
A. filicaulis Fisch. et Mey.	Oxyglottis		16	Ledingham (60). U.S.S.R.
A. finitimus Bge.	Alopecias		16	Rever (61). Iraq.
A. flexuosus Dougl.	Flexuosi	11		Ledingham (57). Canada.
A. frigidus (L.) Bge.	Cenanthrum		16	Løve & Løve (44). Canada.
			16	Ledingham (60). Europe.
A. fruticosus Pall.	Xiphidium		16	Ledingham (60). Spain.
A. fuhsii Freyn et Sint.	Megalocystis		64	Ledingham (60). U.S.S.R.
A. galega			32	Ledingham (60). Kenya.
A. galegiformis L.	Dilotheca	8		Kreuter (29,30), U.S.S.R.
			16	Ledingham (60). Europe.

Species	Section	n	2n	Reference and Species Locatio
A. garbancillo Cavanilles			26	Krapovickas & K. (51). Argentina
A. gilviflorus Sheld. = A. triphyllus Pursh	Triphylli	12		Ledingham (57). Canada.
A. globiceps Bge.	Alopecias		16	Rever (61). U.S.S.R.
A. glycyphyllus L.	Glycyphyllus		16	Tschechow (30). U.S.S.R.
			16	Ledingham (60). Europe.
		8		Larsen (55). Med. Europe.
A. gombiformis Pomel			16	Reese (57). Africa.
A. goniatus Nutt.	Hypoglottides	8		Ledingham (57). Canada.
			16	Ledingham (61). Canada.
A. granatensis Lge.			16	Ledingham (16). Portugal
A. grayi Parry	Podo-Sclerocarpi	22		Vilkomerson (43). U.S.A.
A. gypsodes Barneby	Sarcocarpi		24	Head (57). U.S.A.
A. gyzensis DC	Harpilobus		48	Rever (61). Iraq.
A. hamosus L.	Epiglottis		48	Tschechow (30). U.S.S.R.
		24		Kreuter (30). N. Africa.
A. haydenianus Gray	Bisulcati	12		Vilkomerson (43). U.S.A.
A. heterodontus Boriss.	Brachycarpus		16	Rever (61). U.S.S.R.
A. hispidulus DC	Ankylotus		16	Rever (61). Egypt.
A. hissaricus Lipsky	Proselius		16	Rever (61). U.S.S.R.
A. hypoglottis L.	Eu-Hypoglottis		16	Tschechow (30). Europe.
A. hypoleucus Schauer	Micranthi		28	Rever (61). U.S.A.
A. illyricus Bernh.	Proselius		16	Rever (61). Yugoslavia
A. incanus L.	Podochreati		16	Lorenzo & Garcia (50). Spain.
A. inflexus Dougl. ex Hook.	Argophylli		22	Head (57). U.S.A.
A. interpositus Boriss.	Onobrychium		16	Rever (61). U.S.S.R.

Species	Section	n	2n	Reference and Species Locatio
A. iskanderi Lipsky	Xiphidium		16	Rever (61). U.S.S.R.
A. joergensenii Johnston			26	Krapovickas & K. (51). Argentina.
A. kahiricus DC.	Eremophysa		16	Rever (61). Israel.
A. karakugensis Bge.	Ammodendron	8		Tischler (38). U.S.S.R.
A. kentrophyta Nutt. = A. montanus Nutt.	Homalobi		24	Ledingham (60). Canada.
A. kurdaicus Saposhn.	Cystium		32	Rever (61). U.S.S.R.
A. lagurus Willd.	Hymenostegis		32	Rever (61). U.S.S.R.
A. languginosus Kar. et. Kir.	Erionotus		16	Rever (61). U.S.S.R.
A. lasiosemius Boiss.	Aegacantha		16	Rever (61). U.S.S.R.
A. lentiginosus Dougl. ex Hook.	Inflati		22	Head (57). U.S.A.
var. lentiginosus				
var. palans Jones		11		Vilkomerson (43). U.S.A.
var. variabilis Barneby			22	Ledingham (60). U.S.A.
A. leontinus Wulfen	Onobrychium		32	Rever (61). Switzerland.
A. leptocarpus T. & G.	Leptocarpi	13		Turner (56). U.S.A.
A. leucacantus Boiss.	Chronopus		16	Rever (61). Egypt.
A. leucopsis (T & G.) Torrey	Inflati	11		Snow (59). U.S.A.
			22	Ledingham (60). U.S.A.
A. limatus Sheldon	Preussii	12		Vilkomerson (43). U.S.A.
A. lindheimeri Gray	Leptocarpi		24	Ledingham (60). U.S.A.
A. litvinovii Lipsky	Eremophysa		16	Ledingham (60). U.S.S.R.
			16	Rever (61). U.S.S.R.
A. lonchocarpus Torr.	Lonchocarpi	11		Vilkomerson (43). U.S.A.
A. longiflorus Pall.	Myobroma	8		Tischler (38). U.S.S.R.
A. longipetiolatus M. Pop.	Ammodendron		16	Rever (61). U.S.S.R.

Species	Section	n	2n	Reference and Species Locatio[n]
A. lotiflorus Hook.	Lotiflori		26	Ledingham (60). Canada.
A. lusitanicus Lam.	Erophace		16	Ledingham (60). Portugal
A. macronyx Bge.	Myobroma		16	Rever (61). U.S.S.R.
A. macropelmatus Bge.	Myobroma		16	Rever (61). Iraq.
A. macrourus Fisch. et Mey.	Malacothryx		32	Rever (61). U.S.S.R.
A. massiliensis Lam.	Melanoceris		16	Kreuter (30). S. W. Europe
		8		Kreuter (31).
A. maximowiszii Trautv.	Eremophysa		16	Rever (61). U.S.S.R.
A. membranaceus (Fisch.) Bge.	Cenanthrum		16	Tschechow (30). U.S.S.R.
			16	Rever (61). U.S.S.R.
A. miser Dougl. var. serotinus (Gray) Barneby	Inflati		22	Ledingham (60). Canada.
A. missouriensis Nutt.	Argophylli	11		Ledingham (57). Canada.
A. mollis Bieb.			16	Kachidse (Tischler '27). Caucasus, Persia.
A. mollissimus Torr.	Mollissimi		24	Head (57). U.S.A.
			22	Ledingham (60). U.S.A.
			26	Johnston (59). unpub.
A. mongholicus Bunge	Cenanthrum		16	Rever (61). N. Europe.
A. monspessulanus L.	Proselius	8		Kreuter (29, 30).
			16	Ledingham (60). S. Europe
A. mossulensis Bge.	Onobrychium		32	Rever (61). Iraq.
A. narbonensis Gouan.	Glycyrrizi		16	Tschechow (35). Spain.
A. neglectus (T. & G.) Sheld. = A. cooperi Gray	Uliginosi		22	Ledingham (60). Canada.
A. nigrescens Nutt.	Didymocarpi	11		James (51). U.S.A.
A. nigrimontanus M. Pop.	Chaetodon Bge.		32	Rever (61). U.S.S.R.
A. nuttallianus DC. var. nuttallianus	Leptocarpi		22	Ledingham (60). U.S.A.

Species	Section	n	2n	Reference and Species Locatior
A. nutzotinensis Rous.	Gynophoraria		22	Ledingham (60). Alaska.
A. occidentalis (Watson) Jones	Alpini		32	Ledingham (60). Canada.
A. odoratus Lam.	Euodmus		64	Ledingham (60). Spain.
A. onobrychis L.	Onobrychis		64	Tschechow (35). U.S.S.R.
			64	Ledingham (60). N. Europe.
A. oocalycis Jones	Bisulcati	12		Vilkomerson (43). U.S.A.
A. oocarpus Gray	Inflati	11		Snow (59). U.S.A.
A. oroboides Horn.	Orobella		8	Tischler (38). U.S.S.R.
A. osterhouti Jones	Lonchocarpi		11	Vilkomerson (43). U.S.A.
A. pachypus Greene	Podo-Sclero-carpi		22	Head (57). U.S.A.
A. pallasii Spreng.		8		Tischler (38).
A. palmyrensis Post	Platyglottis		16	Rever (61). Iraq.
A. pattersoni Gray	Preusii	12		Vilkomerson (43). U.S.A.
A. pectinatus Dougl.	Podo-Sclero-carpi			Vilkomerson (43). U.S.A.
		11		
		11		Ledingham (57). Canada.
			22	Ledingham (60). Canada.
A. pehuenches Nieder-lein			22	Ledingham (60). Argentina.
A. penduliflorus Lam.	Cenanthrum		16	Rever (61). Europe.
A. pentaglottis L.	Pentaglottis	14		Senn (38). N. Africa
			28	Ledingham (60). Portugal
			28	Rever (61). Portugal.
A. peregrinus Vahl.	Platyglottis		16	Rever (61). Egypt.
A. peterfii Jav.	Calycocystis		64	Rever (61). Hungary.
A. physocarpus Lbd.	Cystium	8		Tischler (38). U.S.S.R.
A. physodes L.	Cystium		16	Ledingham (60). U.S.S.R.
A. platyphyllus Kar. et Kir.	Proselius		16	Rever (61). U.S.S.R.
A. platyraphis Fisch.	Myobroma		16	Rever (61). Iraq.

Species	Section	n	2n	Reference and Species Location
A. podocarpus C.A. Mey.	Malacothryx		16	Ledingham (60). Spain.
A. pomonensis Jones	Inflati	11		Snow (59). U.S.A.
A. ponticus Pall.	Alopecias		64	Rever (61). Europe.
A. praelongus Sheldon	Preusii	12		Vilkomerson (43). U.S.A.
A. preussii Gray	Preussii	12		Vilkomerson (43). U.S.A.
A. pterocarpus Watson	Podo-Sclero-carpi	11		Vilkomerson (43). U.S.A.
A. pulsiferae A. Gray	Inflati		24	Ledingham (60). U.S.A.
A. purpureus Fom.	Proselius		16	Rever (61). Poland.
A. purshii Dougl. ex Hook. var. glareosus (Dougl. ex Hook.) Barneby	Argophylli		22	Head (57). U.S.A.
var. purshii			22	Head (57). U.S.A.
A. racemosus Pursh.	Galegiformes	12 12		Vilkomerson (43). U.S.A. Ledingham (57). Canada.
A. rafaelensis Jones		11		Vilkomerson (43). U.S.A.
A. retamocarpus Boiss. et Hohen.	Cartilaginella		16	Ledingham (60). U.S.S.R.
A. richardsonii Sheldon	Hemiphragmium		48	Rever (61). U.S.S.R.
A. riparius Barneby			24	Head (57). U.S.A.
A. robbinsii A. Gray	Alpini		16	Ledingham (16). Europe.
A. römeri Simk.			ca.169	Rever (61). Hungary
A. rytilobus Bunge	Oxyglottis		16	Ledingham (60). U.S.S.R.
A. sabulosus Jones	Preussii		26	Rever (61). U.S.A.
A. schahrudensis Bge.	Alopecias	8	16	Tischler (38). Rever (61). U.S.S.R.
A. schelichovii Turcz.	Euodmus		16	Rever (61). Hungary
A. scheremetevianus B. Fedtsch.	Scheremete-viana		16	Rever (61). U.S.S.R.

Species	Section	n	2n	Reference and Species Location
A. schimperi Boiss.	Oxyglottis		16	Rever (61). Iraq.
A. schmalhausenii Bge.	Sewerzowia		16	Rever (61). U.S.S.R.
A. schrenkianus Kar. et Kir.	Microcystis		16	Rever (61). U.S.S.R.
A. schugnanicus B. Fedtsch.	Brachycarpus		16	Rever (61). U.S.S.R.
A. sclerocarpus Gray	Podo-Sclero-carpi	11		Vilkomerson (43). U.S.A.
			22	Head (57). U.S.A.
A. scorpioides Pourr. ex Willd.		24		Tschechow (35). Spain
A. sealei Lepage			16	Ledingham (60). Alaska.
A. secundus DC.	Cenanthrum		48	Sakai (33, 34). S. Siberia.
A. sempervirens Lam.	Acanthophace		16	Rever (61). Switzerland.
A. sesameus L.	Oxyglottis	8		Kreuter (30).
			16	Rschechow (30). W. Med.
A. sesamoides Boiss.	Oxyglottis		16	Rever (61). U.S.S.R.
A. sheldonii (Rydh.) Barneby	Reventi-Arrecti		24	Head (57). U.S.A.
A. sieberi DC	Chronopus		16	Rever (61). Egypt.
A. sieversianus Pall.	Lithoon		16	Ledingham (60). U.S.S.R.
A. sikkimensis Benth. ex Bunge		8		Tschechow (35). Himalayas
A. sinicus L.	Lotidium	8		Kawakami (30). Japan.
			16	Suquira (31). Japan.
			16	Rever (61). Japan.
A. sirinicus Ten. ssp. genargenteus Brig.			16	Contandriopoulos (57). Corsica.
A. skornjakovii B. Fedtsch.	Cystium		16	Rever (61). U.S.S.R.
A. somalensis Taub. ex Harms			20	Ledingham (60). Kenya
			20	Rever (61). Kenya.

Species	Section	n	2n	Reference and Species Locatior
A. spaldingii Gray	Chaetodontes		24	Head (57). U.S.A.
A. spatulatus Sheld.	Homalobi	12		Ledingham (57). Canada.
A. stenanthus Bge.	Hololeuce		16	Rever (61). U.S.S.R.
A. stenophyllus T & G.	Homalobi		12	Head (57). U.S.A.
A. striatus Nutt.	Hypoglottides	16		Ledingham (57). Canada.
A. succumbens Dougl. ex Hook.	Malaci		24	Head (57). U.S.A.
A. sulcatus L.	Craccina	8	16	Tischler (38). Siberia. Ledingham (60).
A. suluklensis Freyn. et Sint.	Malacothrys		48	Rever (61). U.S.S.R.
A. tenellus Pursh.	Homalobi	12		Ledingham (57). Canada.
A. terlinguensis Cory	Micranthi		24	Rever (61). U.S.A.
A. tetrapterus Gray	Podo-sclero-carpi	11		Vilk. (43). U.S.A.
A. tibetanus Benth.	Eu-Hypoglot-tis		16	Rever (61). U.S.S.R.
A. toanus Jones	Podo-sclero-carpi	11		Vilk. (43). U.S.A.
A. tribuloides Del.	Oxyglottis		16	Rever (61). Iraq.
A. tugarinovii N. Basil	Hemiphragm-ium		48	Rever (61). U.S.S.R.
A. turbinatus Bunge	Alopecias		16	Ledingham (60). U.S.S.R.
A. turkestanus Bge.	Christianop-sis		16	Rever (61). U.S.S.R.
A. ugamicus M. Pop.	Xiphidium		82	Rever (61). U.S.S.R.
A. uliginosus L.	Euodmus	8	64	Tschechow (35). U.S.S.R. Ledingham (60). U.S.S.R.
A. umbellatus Bunge	Cenanthrum		16	Ledingham (60). Alaska.
A. unifoliatus Bge.	Ammondendron		16	Ledingham (61). U.S.S.R.

Species	Section	n	2n	Reference and Species Locatio[n]
A. uninodus M. Pop. & Vved.	Harpilobus		16	Rever (61). U.S.S.R.
A. utriger Pall.	Myobroma		16	Ledingham (60). U.S.S.R.
A. venosus Hochst. ex A. Rich.			16	Ledingham (60). Africa.
A. verus Oliv.	Platonychium		64 64	Tschechow (35) Rever (61). W. Iran.
A. vesicarius L.	Cystodes		16	Tschechow (35). U.S.S.R.
A. vexilliflexus Sheld.	Inflati	11		Ledingham (58). Canada.
A. viciifolius Hulten	Eu-Hypoglottis		32	Ledingham (60). Alaska.
A. vimineus Pall.	Xiphidium	24		Tschechow (35). U.S.S.R.
A. vulpinus Willd.	Alopecias	8		Kreuter (29, 30). U.S.S.R.
A. wootonii Sheld.	Inflati		22 24	Ledingham (60). U.S.A. Turner (59). U.S.A.
A. wrightii Gray	Leptocarpi		22	Ledingham (60). U.S.A.
A. xanthomeloides E. Kor. & M. Pop.	Macrocystis		16	Rever (61). U.S.S.R.
A. xipholobus M. Pop.	Cytisodes		16	Rever (61). U.S.S.R.
A. yukonis M. E. Jones	Debiles		24	Ledingham (60). Yukon.
Oxytropis arctica R. Br. ssp. taimyrensis Jurtz.	Orobia		64	Rever (61). U.S.S.R.
O. argentata (Pall.) Pers.	Orobia	8		Tschechow (35). U.S.S.R.
O. argentea Pers.			48	Rever (61). Finland.
O. baicalia (Pall.) Pers.	Baicalia	8		Tschechow (35). U.S.S.R.
O. besseyi (Rydb.) Blank		8		Ledingham (58). Canada.

Species	Section	n	2n	Reference and Species Location
O. campestris (L.)DC.	Orobia		48	Jalas (50).
			32	Ledingham (57). Canada
			48	Ledingham (60). Can. Europe.
			32	Ledingham (60). Canada.
O. chiliophylla Royle	Polyadena		16	Rever (61). U.S.S.R.
O. deflexa (Pall.) DC.	Mesogaea	8		Ledingham (57). Canada.
			16	Ledingham (60). Can. U. S.A.
O. foetida (Vill.) DC.			48	Rever (61). Europe.
O. glabra (Lam.) DC.	Mesogaea	8		Tschechow (35). U.S.S.R.
O. halleri Bunge	Orobia		16	Tschechow (30). U.S.S.R.
O. japonica Maxim.			16	Rever (61). Japan.
O. karataviensis N. Pavl.	Physocarpon		16	Rever (61). U.S.S.R.
O. kopetdagensis Gontsch.	Mesogaea		16	Ledingham (60). U.S.S.R.
O. lambertii Pursh.		24		Ledingham (57). Canada.
O. lapponica (Wahl.) Gay	Protoxytropis	24		Tschechow (35). Europe, U.S.S.R.
O. megalantha Boissieu			32	Rever (61). Japan.
O. mertensiana Turcz.	Caeciabia		16	Rever (61). U.S.S.R.
O. montana DC.			16	Favarger (53). Europe.
O. nigrescens (Pall.) Fisch.	Arctobia		16	Rever (61). U.S.S.R.
O. podocarpa Gray			16	Ledingham (60). Canada
O. rishiriensis Matsum			ca.53	Sakai (33-34). Japan.
O. schischkinii Vass.	Orobia		96	Rever (61). U.S.S.R.
O. sericea Nutt. var. spicata (Hook.) Barneby		24		Ledingham (57). Canada.
			48	Ledingham (60). Canada.
O. splendens Dougl.		8		Ledingham (57). Canada.
			16	Ledingham (60). Canada.

Species	Section	n	2n	Reference and Species Location
<u>O</u>. <u>sulphurea</u> (Fisch.)	Orobia		48 16	Ledingham (60). Europe. Rever (61). U.S.S.R.
<u>O</u>. <u>trichocalycina</u> Bge.	Ptiloxytropis		16	Rever (61). U.S.S.R.
<u>O</u>. <u>uralensis</u> Pall.			16	Tschechow (30).
<u>O</u>. <u>uralensis</u> Ldb.	Orobia		16	Rever (61). Austria.
<u>O</u>. <u>vaginata</u> Fisch.	Ortholoma		16	Tschechow (30). Siberia.
<u>O</u>. <u>viscida</u> Nutt.			16	Ledingham (58). Canada.