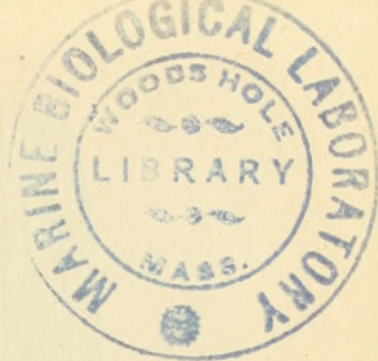


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ENDEMISM IN *CREPIS*

BY

ERNEST B. BABCOCK

*Professor of Genetics  
University of California*

I. INTRODUCTION

ONE RESULT of the extensive investigations on the genus *Crepis* has been the formulation of a fairly definite hypothesis concerning the origin, development and migrations of this essentially monophyletic group of plants. This hypothetical history of the one hundred and ninety-six species of *Crepis* has been found to be consistent with a great mass of other evidence concerning the origin and migrations of floras in the northern hemisphere. A review of this evidence together with a detailed discussion of the data on *Crepis* will be presented in a monograph which is in press.

The criteria of phylogenetic relations in *Crepis* represent five different disciplines. The primary basis for classifying all the species into twenty-seven sections and arranging the sections in an approximate phyletic series is comparative morphology. Second in importance have been the data on chromosome numbers in one hundred and thirteen of the species (cf. Babcock and Jenkins, 1943). Thirdly, the cytogenetic analysis of certain interspecific hybrids has confirmed the conclusions reached concerning the phyletic relations of the parent species as determined on the basis of comparative morphology and chromosome numbers, and has revealed the evolutionary process by which reduction in chromosome number in the series 6-5-4-3 has been accomplished (cf. Babcock, 1942, pp. 176-178; Tobgy, 1943). Fourthly, purely genetic data on many interspecific hybrids have substantiated the grouping of



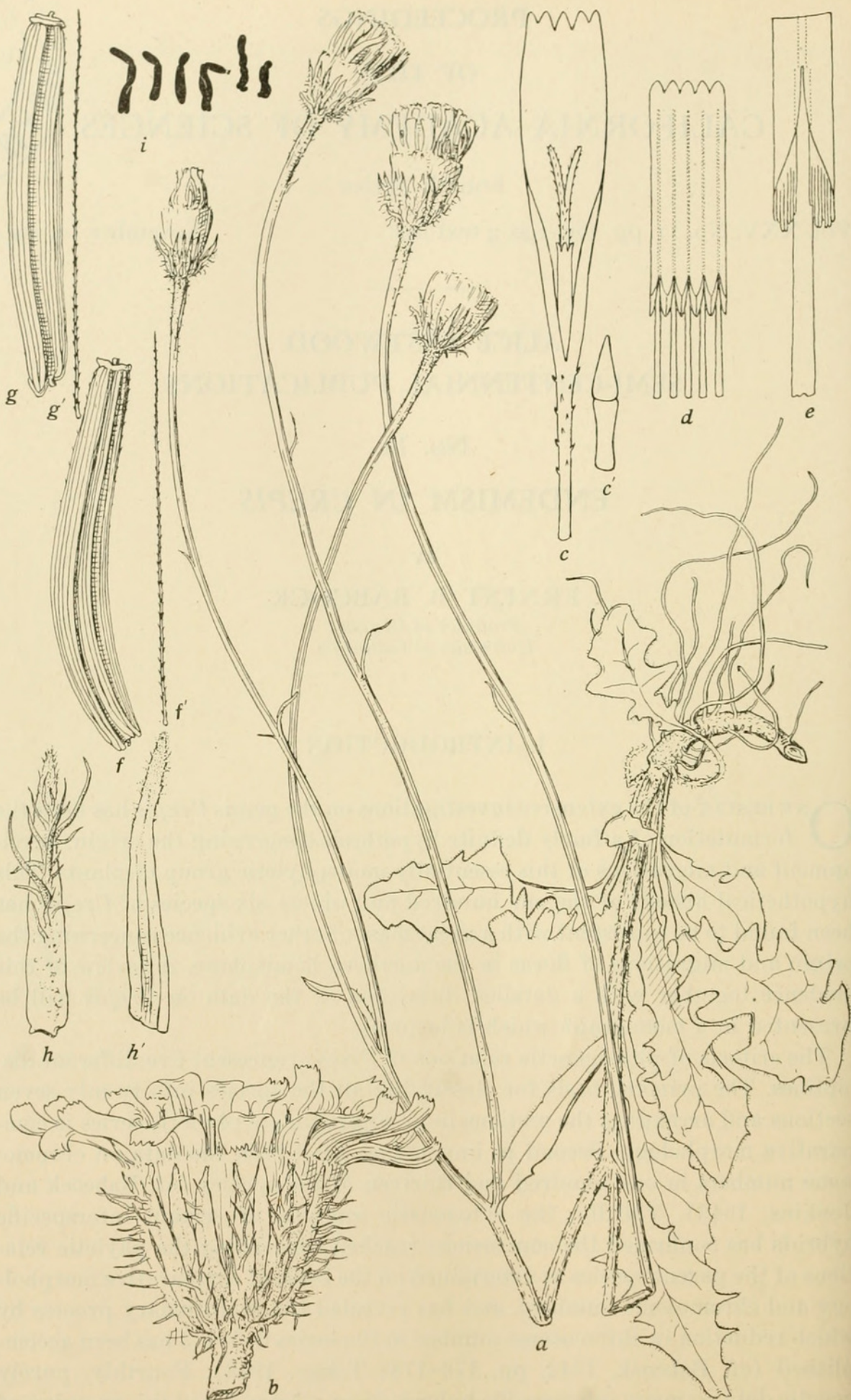


Fig. 1. *Crepis geracioides* Hausskn. a, plant,  $\times \frac{1}{2}$ ; b, flower-head,  $\times 2$ ; c, a floret lacking the ovary,  $\times 4$  ca.; c', trichome from the corolla-tube,  $\times 100$  ca.; d, anther-tube slit and opened out,  $\times 8$  ca.; e, detail of anther-appendages,  $\times 32$  ca.; f, g, two achenes and a pappus-seta from each,  $\times 8$  ca.; h, h', two inner involucre bracts showing outer and inner faces respectively,  $\times 4$  ca.; i, haploid set of chromosomes,  $\times 1500$ .



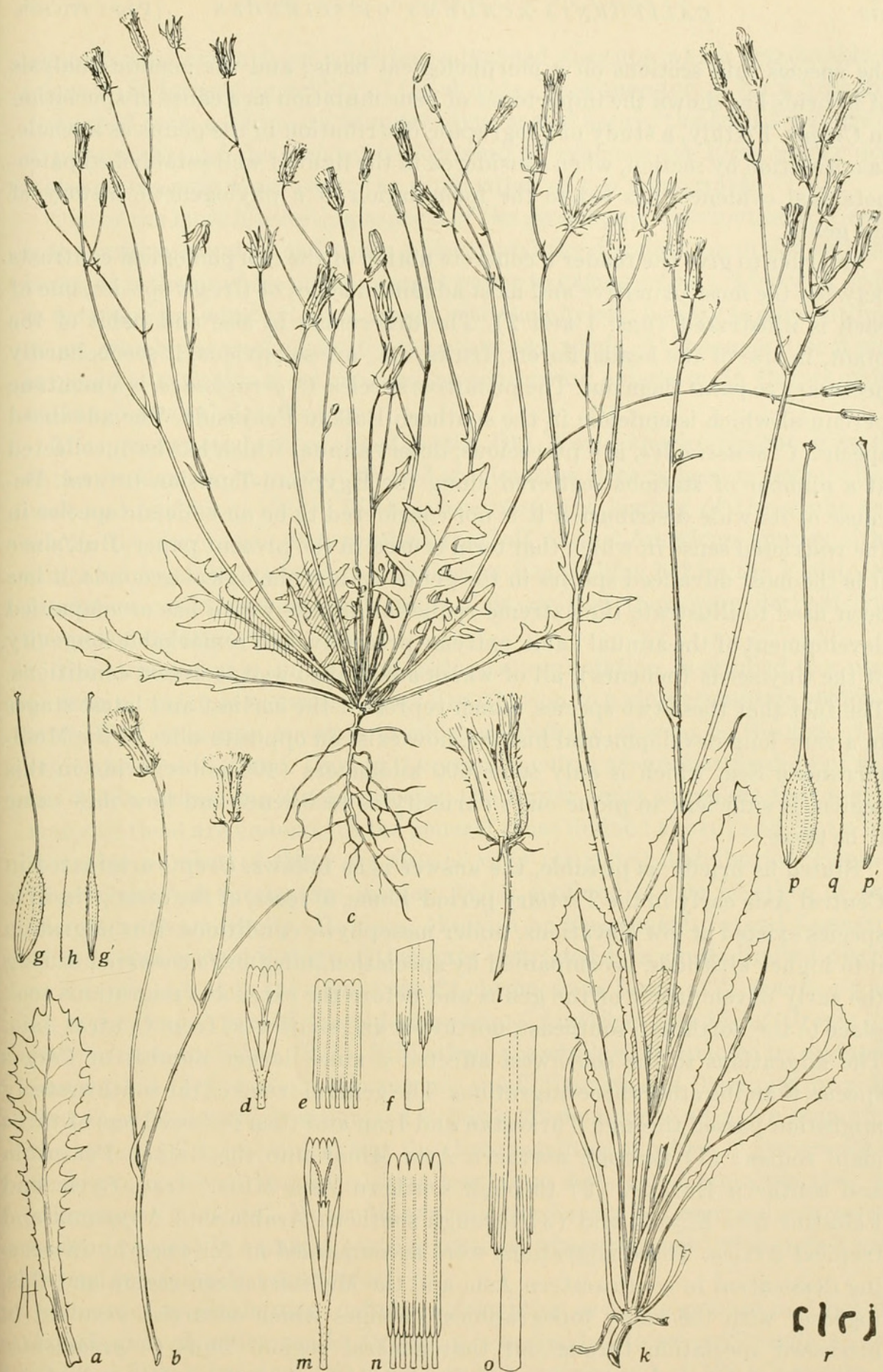


Fig. 2. *Crepis senecioides* Delile. a, b, c and k, plants and parts,  $\times \frac{1}{2}$ ; d, m, florets lacking the ovary,  $\times 4$  ca.; e, n, anther-tubes slit and opened out,  $\times 8$  ca.; f, o, details of anther-appendages,  $\times 32$  ca.; g, h, p, q, achenes and single pappus-setae,  $\times 8$  ca.; r, haploid set of chromosomes,  $\times 1500$ .



the species into sections on a morphological basis; and the genetic analysis of hybrids has shown the importance of gene mutation as a cause of speciation in *Crepis*. Fifthly, a study of geographic distribution in the genus as a whole, taken section by section, when considered in the light of well-established paleobotanical evidence, has led to the formulation of a phylogenetic history of the genus.

In order to give the reader a concrete notion of the morphological contrasts between the most primitive and most advanced types of *Crepis* species, one of each is illustrated (figs. 1 and 2). The differences in size and habit of the plant, in size of the heads, florets, fruits, etc., are so obvious, it seems hardly necessary to point them out. The primitive species, *C. geracioides*, is a montane perennial which is endemic in the southern Balkan Peninsula. The advanced species, *C. senecioides*, is a precocious, desert annual which has been collected at a number of stations scattered along the Egyptian-Tunisian littoral. Because of its wide distribution it is not considered to be an endemic species in the restricted sense in which that term is used in the present paper. But, since it is the most advanced species in the genus on morphological grounds, it has been used to illustrate the extreme reduction in size which has accompanied development of the annual habit, extreme precocity, and remarkable longevity of the tiny seeds (achenes), all of which adapt it so well to desert conditions. The fact that these two species, which represent the earliest and latest stages in a very long developmental history, now exist on opposite sides of the Mediterranean Sea, which is only some 600 kilometers (400 miles) wide in this region, is sufficient to pique one's curiosity as to whence and how they came to be there.

Stated as briefly as possible, the answer is as follows. *Crepis* originated in Central Asia early in the Tertiary period. Some, at least, of the most primitive species existed at low elevations, under mesophytic conditions. But migration into higher altitudes, accompanied by speciation, must have occurred during the early development of the genus and before the extensive migrations took place to the northeast, southeast, northwest and southwest from Central Asia. The migrations to the southwest affected a much larger number of *Crepis* species than the other three migrations. The general trend of the southwesterly migration passed through Turkestan and Iran and then followed one of three main routes: (1) through northern Asia Minor into the Balkan Peninsula and southern Europe; (2) through southern Asia Minor, Iraq, Syria and Palestine into Egypt; and (3) through southern Arabia into Abyssinia and tropical Africa. These migrations were accompanied or followed by increasing dessication in southwestern Asia and the Mediterranean region and this, together with the many topographical changes which occurred, resulted in increased speciation throughout that general region. Thus *C. geracioides* almost certainly migrated from Central Asia around the south end of the Caspian Sea, through northern Asia Minor, into the Balkan Peninsula where it still exists in three localities. But *C. senecioides* almost certainly developed



where it now exists from some less advanced ancestor which was unable to tolerate the increasing aridity of the climate. That ancestor, in turn, probably developed from a still more primitive type somewhere in the Iran-Iraq region. A presentation of the general background of evidence for these rather dogmatic statements must await the publication of the monograph.

One of the most interesting aspects of the geographic distribution of *Crepis* is the large amount of endemism present and the distribution of the endemic areas. It is the purpose of the present paper to examine this evidence in order to determine to what extent it agrees with the phyletic history briefly outlined above, which was worked out for the genus as a whole. At the same time it may be possible to derive some conclusions concerning endemism in *Crepis* which will have general significance.

The present study is confined to the Old World species inasmuch as the data on endemism in the New World species have already been reported (Babcock and Stebbins, 1938). With reference to the history of the genus as a whole, the conclusion was reached that all of the American species either migrated from Asia across the Beringian land-bridge before the Pleistocene glaciation could prevent such migrations, or that they were derived from species of Asiatic origin.

The term endemic, in its usual biological connotation, is applied to a plant or animal which is restricted in its distribution to a single country, region or area. This definition becomes much more definite as soon as the size of the region or area is stated. During the years spent in accumulating data of various kinds concerning *Crepis* species, the writer came to realize that a great many of them are endemic in the general sense defined above; and that a considerable number of them are also of very restricted distribution. Some of these restricted species are insular, being confined to one or other of such islands as Crete, Sicily, Majorca, Madeira or Fuerteventura and Lanzarote of the Canary Archipelago. Others are restricted to a single limited district on a continent, as in the case of the 22-chromosome forms of *C. monticola* and *C. pleurocarpa*, two of the oldest endemic American species of *Crepis* (cf. Babcock and Stebbins, 1938). Still others are similarly restricted by ecological factors, but they occur in two or more small districts and these may be either near together or widely separated within a given endemic area. An example of the latter is *C. geracioides*; but the three localities at which *C. geracioides* is known to occur are separated by a maximum distance of approximately 150 kilometers (90 miles). Hence this species can hardly be described as a *narrow* endemic except in a purely relative sense, as when compared with such a widespread species as *C. senecioides*.

In order to obtain more definite information as to the amount and possible significance of endemism in *Crepis*, it was decided to set arbitrarily a lower limit of fifty kilometers (30 miles) and an upper limit of 150 kilometers (90 miles); and to classify all the species whose maximum straight-line distance between known localities falls within the lower limit as "narrow A"; all those



whose maximum distance between known localities exceeds the upper limit as "wider"; while those falling between the two limits were classed as "narrow B." It was found that there were so few species in the "narrow B" group that, for the sake of simplicity, the "narrow B" and "wider" groups were lumped together, thus recognizing only two categories, "narrow" and "wider," with the dividing line at 50 kilometers.

On this basis it was found that there are forty-eight species of *Crepis* for which the available data indicate a "narrow" distribution. Twenty-eight of these are known from only one locality while the other twenty are known from two or more localities. Of the twenty-eight that are known from a single locality, twenty-four are known to the writer from just one collection; but the other four are known to have been collected several times at the one locality. Three of these four localities are mountain peaks in Greece; the other is the eastern promontory of Madeira Island. The twenty-four localities at which only a single collection has been made are mostly in regions which have been less thoroughly explored botanically, such as Asia Minor, the Caucasus, Turkestan and tropical Africa. Many of these localities are in mountainous country and some are mountain peaks. Since many of the "wider" endemics are known to be very local in their distribution, and half of the "narrow" ones are known from two or more collections, it is fairly probable that the majority of the species known from only one collection will turn out eventually to be actually "narrow" as here defined. At any rate the purposes of the present paper can be served better by recognizing them as "narrow" than by ignoring them.

Classification of the remainder of the *Crepis* species as endemic or not endemic was accomplished by defining a series of endemic areas and then by accepting as endemic only those known to be restricted to a single area. Many of these areas are widely recognized as rich in endemic species of plants. By this method ninety-one species were selected as "wider" endemics. This does not mean that these species are continuously distributed over a district more than 150 km. (90 miles) in diameter. On the contrary these "wider" endemics are all more or less local in their distribution; although a few are fairly abundant in certain districts. Thus in the case of *C. geracioides* it happens that the three known localities are about 150 kilometers distant from one another; whereas *C. terglouensis*, another very primitive endemic, is known from at least twenty high alpine stations ranging from south-central Switzerland to central Tirol and Upper Austria. In marked contrast with these are such insular species as *C. cretica* and *C. canariensis* which are abundant on the islands where they exist. A few species have been omitted which occur mostly in one endemic area but are also represented in another and hence, on a less restricted criterion, might have been considered as endemic. Interesting examples are *C. pygmaea*, a very primitive 12-chromosome species of Spain, the Pyrenees, the southwestern Alps and northern Italy; *C. smyrnaea*, another 12-chromosome primitive species known from only three localities in southern



Greece and western Asia Minor; *C. pontana*, the most primitive 10-chromosome species of *Crepis*, which occurs from the eastern Alps to the western part of the Balkan Peninsula; and *C. albida*, the next most primitive 10-chromosome species which is polymorphic and is distributed from the Grand Atlas Mts., in Morocco through Spain, the mountains of southern France and the Maritime Alps. It becomes difficult to know where to draw the line, if one begins to go beyond the limits of a single endemic area. But, on this restricted basis, there are still one hundred and thirty-three endemic species which is 72 per cent of the one hundred and eighty-five Old World species.

## II. THE DISTRIBUTION OF THE ENDEMIC REGIONS AND AREAS FOR *CREPIS*

The endemic regions and areas for *Crepis* are defined in Table 1 and shown on the accompanying map (fig. 3). On this map the large size of the tropical African area (no. 19) will be one of the first things to catch the attention. It should be emphasized that, in the latter area, all of the eighteen endemic species found there are extremely local in distribution. All but three occur on only one or two mountains or in a single mountain range. These mountains and ranges are shown as solid circles or narrow ellipses on the map. The other three species are known from only single stations which are at low elevation and these are shown as solid squares on the map. Following is a key to the symbols used to designate these locations in area No. 19 and three others in area No. 10.

The long winged-shaped ellipse in area No. 10 is the Pamir-Ferghana-Altai system of mountains.

### KEY TO MAP SYMBOLS

Regions are indicated by Roman numerals. Areas are indicated by Arabic numerals.

*Mountains shown by solid circles and ellipses:*

- AT. Ala-tau Mts., Central Asia.
- CH. Mt. Chirinda, southeastern Africa.
- DA. Darvas Mts., eastern Russian Turkestan.
- CU. Congo-Uganda plateau north of Lake Kiwu, Africa.
- HI. Himalaya Mts., Kashmir region, high alpine.
- KE. Mt. Kenya, eastern tropical Africa.
- KI. Mt. Kilimanjaro, eastern tropical Africa.
- KU. Mountains south of Lake Kiwu, tropical Africa.
- MC. Mt. Cameroon, western tropical Africa.
- ME. Mt. Meru, adjacent to Kilimanjaro.
- NY. Mountains of Nyasaland and adjacent Congo.
- RM. Mt. Rungwe and Mt. Mbeya, tropical Africa.
- UK. Urundi Province, Kisozi, tropical Africa.
- UL. Uluguru Mts., Tanganyika Prov., Africa.
- UT. Ulu-tau Mts., northern Russian Turkestan.



*Single lowland stations in Africa:*

- EC. Elizabethville, southeastern Belgian Congo.  
 FU. Fort Portal, Uganda.  
 CA. Cului, Angola.

TABLE 1

## ENDEMIC REGIONS AND AREAS FOR OLD WORLD CREPIS

<i>Regions</i>	<i>Areas</i>
I. Southwestern Europe; Alps; north-western Morocco	1. S. Spain and N.W. Morocco 2. N.E. Spain and W. France 3. European Alps
II. Balkan Peninsula	4. Balkan Peninsula
III. Asia Minor; Syria-Palestine; Crimea	5. Asia Minor 6. Syria and Palestine 7. Crimea
IV. Caucasus; Iran	8. Caucasus region 9. Iran
V. Turkestan-Pamir-Altai region	10. Turkestan (E. and N. Russian) and the Pamir-Altai mountains
VI. Northwestern India	11. N.W. Himalaya Mountains, high alpine 12. N.W. India-Baluchistan, low montane
VII. Southeastern Asia	13. S.E. Asia (= S.E. Tibet, S.W. China, N. Burma, Laos, Annam)
VIII. Eastern Siberia	14. E. Siberia (Okhotsk district)
IX. Northern Japan	15. Hokkaido-Sakhalin
X. Abyssinia; Eritrea; southwestern Arabia	16. S.W. Arabia in Yemen Province 17. Eritrea 18. N. Abyssinia, mountains
XI. Africa, tropical	19. Africa, tropical (isolated localities)
XII. Lybia-Morocco-Cadiz (littoral); southern and western maritime Italy and southern France; Madeira and Canary Islands	20. Lybia (littoral) 21. Tunisia (middle and southern) 22. E. Algeria (littoral) 23. S. Italy and Toscana, Sicily, Sardinia, Corsica; S. France 24. W. Algeria, N. Morocco, Cadiz (mostly littoral) 25. Madeira and Canary Islands

The distribution of the twelve endemic regions defines the east-west distribution of the genus as a whole almost completely, the gaps between the endemic regions being occupied more or less by the various widespread species. In this connection it should be repeated that the total evidence on geographic distribution in *Crepis*, considered in relation to the evidence on phylogeny, definitely indicates that the center of origin and early development of *Crepis* was in Central Asia, in the Altai-Tian Shan mountain region in the north-eastern part of region V (fig. 3); and that the present wide distribution of the genus was accomplished through migration in four general directions from the center. One of these trends was towards the northwest, into what is now Russia. Only five species exist today in northern Europe as a result of that



trend of migration and none of these is endemic. Another migration trend was to the east and northeast, resulting in two endemics in Japan, one in the Okhotsk district of Siberia, (region VIII, fig. 3), and all of the American species. Still another trend was to the southeast, resulting in the nine endemic species found in region VII. Most important of all the migration trends from Central Asia, in terms of the number of species involved, was the southwest-

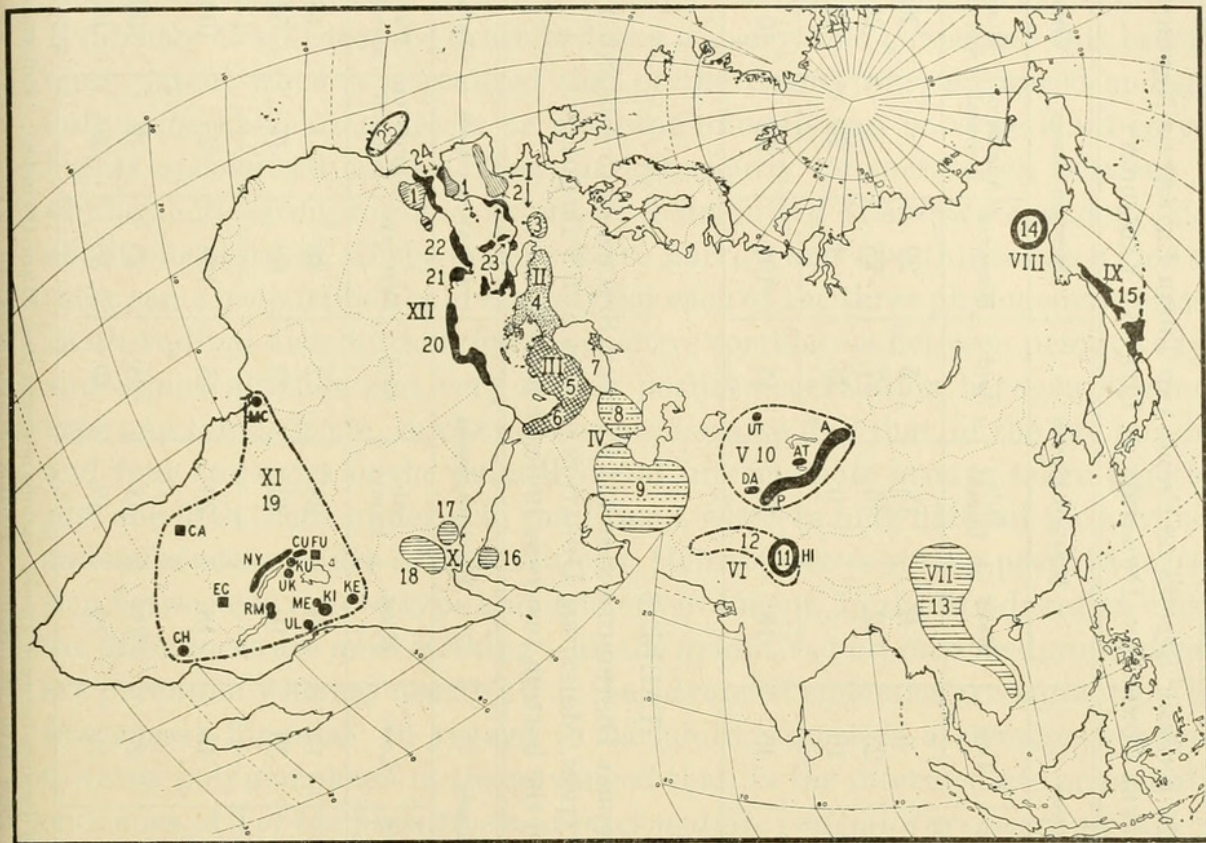


Fig. 3. Map of the Old World showing the endemic regions (Roman numerals) and areas (Arabic numerals) for *Crepis*. (In regions V and XI solid circles indicate single mountains and ellipses, mountain ranges or systems; solid squares indicate single lowland stations. See key to symbols in text.)

erly trend across Turkestan and Iran. From that region the three branches already mentioned led to northwest and tropical Africa; to the Caucasus, Asia Minor and southern Europe; and to the eastern Mediterranean and North African littoral. The point to be emphasized here is that the distribution of the endemic regions for *Crepis* is entirely consistent with the generic history briefly outlined above.

### III. PHYLOGENY AND ENDEMISM IN *CREPIS*

Based on the evidence from comparative morphology and cytogenetics it has been possible to classify all the species of *Crepis* on a relative phylogenetic basis with some degree of assurance. For purposes of the present discussion they have been grouped into three classes, the more primitive, the intermediate, and the more advanced species. In Table 2 are shown the relations of the endemic species in these phylogenetic groups to the size of area occupied



TABLE 2

RELATIONS BETWEEN THE PHYLOGENETIC GROUPS OF 139 ENDEMIC SPECIES OF *Crepis* AND THEIR EXTENT OF NATURAL DISTRIBUTION, ELEVATION, GENERAL MOISTURE CONDITION, DURATION OF LIFE AND VARIABILITY

Phylogenetic groups	Distribution classes		Altitude classes			Moisture classes			Duration classes		Variability classes		Totals
	Narrow	Wider	Alpine	Montane	Low	Moist	Sub-humid	Arid	Perennial	Annual or biennial	Mono-morphic	Poly-morphic	
Primitive.....	11	18	7	18	4	6	18	5	29	..	26	3	29
Intermediate.....	28	47	24	28	23	12	46	17	75	..	61	14	75
Advanced.....	9	20	..	10	19	..	6	23	4	25	17	12	29
Totals.....	48	85	31	56	46	18	70	45	108	25	104	29	133

TABLE 3

RELATIONS BETWEEN THE EXTENT OF NATURAL DISTRIBUTION OF 133 ENDEMIC SPECIES OF *Crepis* AND THEIR PHYLOGENETIC GROUP, ELEVATION, MOISTURE, DURATION OF LIFE AND VARIABILITY

NOTE.—Numbers in the bottom two rows indicate percentages.

Distribution classes	Phylogenetic groups			Altitude classes			Moisture classes			Duration classes		Variability classes		Totals
	Primitive	Inter- mediate	Advanced	Alpine	Montane	Low	Moist	Sub- humid	Arid	Perennial	Annual or biennial	Mono- morphic	Poly- morphic	
Narrow <sup>a</sup> .....	11	28	9	10	25	13	8	28	12	40	8	48	..	48
Wider.....	18	47	20	21	31	33	10	42	33	68	17	56	29	85
Totals.....	29	75	29	31	56	46	18	70	45	108	25	104	29	133
Narrow.....	23	58	19	21	52	27	17	58	25	83	17	100	..	100
Wider.....	21	55	24	25	36	39	12	49	39	80	20	66	34	100

<sup>a</sup> "Narrow endemics," as used here, are species having the maximum distance between known stations not more than 50 km. (30 miles); "wide endemics" have the maximum distance between known stations more than 50 km., and 80 per cent of these have this distance exceeding 150 km. (90 miles).



by each species (narrow or wider), to its altitude class (alpine, montane or low), its moisture classification (as occupying a moist, subhumid or arid environment), its life-duration class (perennial or annual-biennial), and its variability class (monomorphic or polymorphic).

Considering first the totals in the right hand column, it will be noted that twenty-nine of the endemic species are primitive and twenty-nine are advanced, whereas seventy-five, or more than one-half of them, are intermediate. Evidently *Crepis* may be described as a conservative genus and this becomes more patent when it is realized that of the twenty-nine advanced endemics only some half-dozen desert or montane annuals can be considered as very highly specialized species. There is apparently no correlation between the phylogenetic grouping and extent of distribution (narrow *vs.* wider), since about one-third of all the endemics are narrow and two thirds are wider and these same proportions hold roughly for each of the three phylogenetic classes. In altitudinal distribution there is positive correlation between primitive type and alpine altitude and very strong positive correlation between advanced type and low altitude. In the moisture classes we find that, of the one hundred and four endemics in the primitive and intermediate groups taken together, just one-fifth occur under arid conditions, whereas four-fifths of the advanced endemics occur under arid conditions. Hence there is strong positive correlation between advanced type and arid environment. In the life-duration classes the differences are most striking—all the primitive and intermediate endemics are perennial whereas nearly all of the advanced endemics are annual or (in a few cases) biennial. In regard to variability there is a stronger tendency towards polymorphism in the advanced than in the intermediate or primitive endemics. *All of the primitive and intermediate endemics are perennial species and more than four-fifths of them are monomorphic and occur at montane or alpine elevations and under subhumid or moist conditions. Most of the advanced endemics are annual species and two-fifths of them are polymorphic; none occur at alpine elevations and about three-fourths of them are found at low elevations and under arid conditions.*

Having noted the lack of correlation between extent of distribution (as expressed by the arbitrary classes "narrow" and "wider" (and the three phylogenetic groups, it may be of interest to examine the relations between extent of distribution and the other four classifications of endemic *Crepis* species. In Table 3, in order to reveal the relations involved more clearly, the actual numbers, given in the upper two rows, are expressed in the lower two rows as percentages of the respective totals, given in the right-hand column. The totals given in the middle row are merely for the purpose of checking against the other tables. Comparing these percentages, it is clear that there is little or no positive correlation between narrow and wider distribution and phylogenetic grouping. But it is equally clear that there is positive correlation of wider distribution with low altitude and arid climate. As for duration of life and variability, about four-fifths of both the narrow and the wider en-



TABLE 4

RELATIONS OF THE HAPLOID NUMBERS, 6, 5, 4, 3, TO THE PHYLOGENETIC GROUP, EXTENT OF NATURAL DISTRIBUTION, ELEVATION, MOISTURE, DURATION OF LIFE AND VARIABILITY OF 53 ENDEMIC SPECIES OF *Crepis*.

NOTE.—The polyploid endemics *C. ciliata*, *C. incana* and *C. taygetica*, are omitted.

Chromosome numbers	Phylogenetic groups			Distribution classes		Altitude classes			Moisture classes			Duration classes		Variability classes		Totals
	Primi- tive	Inter- mediate	Ad- vanced	Narrow	Wider	Alpine	Mon- tane	Low	Moist	Sub- humid	Arid	Peren- nial	Annual or biennial	Mono- mor- phic	Poly- mor- phic	
<i>n</i> = 6.....	6	3	..	..	9	3	3	3	2	3	4	9	..	7	2	9
<i>n</i> = 5.....	4	2	4	2	8	1	4	5	..	4	6	6	4	5	5	10
<i>n</i> = 4.....	5	13	15	6	27	6	4	23	5	14	14	21	12	22	11	33
<i>n</i> = 3.....	..	..	1	..	1	..	1	..	..	..	1	..	1	..	1	1
Totals.....	15	18	20	8	45	10	12	31	7	21	25	36	17	34	19	53



demics are perennial; whereas all of the narrow endemics are monomorphic, but one-third of the wider endemics are polymorphic.

Considering these facts in the light of the conclusions derived from Table 2, it may be inferred that the advanced, annual endemic species which are polymorphic are mostly of wider distribution and occur at low altitude, under arid conditions. This inference has been verified by reëxamination of the original data. There are twenty-five annual endemic species (Table 2) of which twenty-three occur in an arid climate and all but one of these at low altitude. Only eighteen are known to have a wider distribution; but, of the other seven, six are known as yet only from the type locality and further collections may show that some of these also have a wider distribution.

The contrast between this group of advanced endemics and the strictly alpine endemics is most striking. Of the thirty-one alpine endemics, all are perennial; twenty-nine are monomorphic and only two, polymorphic; while all but one occur under subhumid or moist conditions. Six of them are primitive, and twenty-five intermediate—there are no advanced alpine species. *This means, of course, that the alpine endemics are all relatively old species and adapted to mesophytic conditions; whereas the lowland endemics of advanced type are relatively young species and adapted to xerophytic conditions.*

But the contrast between the two groups does not hold for size of distributional area. Of the thirty-one alpine endemics twenty-one are wider and only ten narrow in distribution. Furthermore, there are ten other alpine species of *Crepis* which are so extensive in geographic distribution that they are not considered to be endemic. For example, *C. conyzaefolia* is a primitive alpine-subalpine species distributed from the Pyrenees to the Balkan Peninsula and in northern Asia Minor, Transcaucasia, northern Persia and the Altai region. Such evidence, together with the prevalence of wide distribution among the alpine endemics, certainly indicates that the *alpine endemics were formerly more widely distributed and have become restricted to their present locations presumably through radical changes in the environment.*

The evidence on chromosome numbers is in good agreement with the foregoing generalizations. In Table 4 fifty-three diploid endemic species are classified opposite their numbers 6, 5, 4, or 3, and in relation to phylogenetic grouping and the other classifications used in the preceding tables. Phylogenetically, the 6-paired endemics are all primitive or intermediate, none are advanced; whereas the 5-paired endemics are about evenly divided among the three groups and the 4-paired endemics are mostly intermediate or advanced. The one 3-paired endemic, *C. fuliginosa*, is advanced, widely distributed, montane, xerophytic, annual, and polymorphic. In distribution all of the 6-paired endemics are wider as well as most of the 5's and 4's; but the small number of narrow endemics that have been examined cytologically may be partly due to difficulties in obtaining them in living condition. The data on altitudinal distribution indicate no correlations except in the 4-paired species which are mostly of low elevation. As for moisture relations, most of the fifty-three



species are about equally divided between subhumid and arid and this holds for each of the chromosome number classes. Under duration of life we find that all of the 6-paired endemics are perennial, whereas about one-third of both 5's and 4's are annual. Obviously reduction in length of life has gone along with reduction in the number of chromosomes. As for variability, there is little difference between the chromosome number classes in the proportion of monomorphic and polymorphic species. The most significant facts derived from this analysis are: (1) *The 6-paired species are mostly primitive and all perennial, but they are about equally distributed among the altitude and moisture classes.* (2) *The 4-paired species are mostly intermediate or advanced and of low elevation, but they are about equally divided between mesophytic and xerophytic environments.* (3) *These facts seem to indicate that adaptation from mesophytic to xerophytic conditions has been going on in this genus over a very long period of time.*

#### IV. THE DISTRIBUTION AND PHYLOGENY OF *CREPIS* ENDEMICS

In Table 5 each of the endemic *Crepis* species is tabulated according to the endemic region in which it occurs and its phyletic, altitude and life-duration class; also the fifty-three endemics that have had their chromosomes counted are tabulated according to chromosome number as well as the region where they occur.

Considering first the primitive endemics, it will be noted that two grades are recognized, A and B. The thirteen species in the A group are definitely more primitive than those of the B group on morphological grounds. Eleven of these most primitive endemics are either alpine or montane, and restricted to southwestern Europe or the Balkan Peninsula or to a few high mountains in tropical Africa. The other two are alpine species, one in the western Himalaya Mountains and the other in the northern islands of Japan. Thus the most primitive *Crepis* endemics are now mostly distributed at great distances from the assumed center of origin for the genus. Since most of the advanced endemics are closer to Central Asia than southwestern Europe, the distribution of the most primitive and most advanced endemics in *Crepis* conforms in general with Matthew's principle of radial distribution of older types from a common center accompanied by the development of more advanced types nearer the center (Matthew, 1915). This conformity with Matthew's principle is also apparent from the distribution of all the species (including the endemics) in several of the more primitive sections of *Crepis*. These facts provide a sound basis for the hypothetical history of *Crepis* which starts with the origin and early development of the genus in Central Asia.

Considering next the totals for the twelve regions (Table 5, left-hand column), it is clear that the greatest concentrations of endemics exist in the Balkan Peninsula, in Asia Minor and adjacent areas, in tropical Africa, and in the Mediterranean littoral. But these four regions differ as to the phylo-



genetic status of their endemics. In the Balkan Peninsula close to one-half of the endemics are intermediate, whereas, one-fourth are primitive (A+B) and one-fourth, advanced. These twenty-six species are similarly divided between montane, alpine and low elevations; the seven advanced species are all annuals. Evidently the highly diversified conditions in that region have favored the persistence of both primitive and intermediate endemics as well as the development of advanced endemics. In Asia Minor and the Mediterranean littoral, however, the endemics are all either intermediate or advanced. But the fact that there are no primitive endemics in Asia Minor is probably due to the generally more arid climate of that region as compared with the Balkan Peninsula as a whole. In tropical Africa, on the other hand, we find just the opposite situation. The eighteen endemics are all either intermediate or primitive; and this is also true of four other tropical African species which are so widely distributed that they are not included here as endemics. This absence of advanced species in tropical Africa probably indicates that the more uniform and favorable conditions of that region have favored the persistence of more primitive types without inducing the development of very advanced types.

Compared with the four regions that are richest in endemics, the following regions have only one-third to one-half as many in each region: southwestern Europe, the Caucasus-Iran region, Abyssinia and adjacent small areas, and southeastern Asia. One of these, the Abyssinian region, differs from the other four in having all the phyletic groups represented. The ten endemics of the Abyssinian region are all montane except the two primitive species which are alpine; and yet four of these montane species are advanced. It will be recalled, however, that certain other advanced species are montane. This is true of the one 3-paired endemic, *C. fuliginosa*, which occurs in southern Greece, and of its 4-paired close relative, *C. cretica*. The three other regions contain only perennial endemics, none of which is advanced, some being intermediate and some primitive. Southwestern Europe and tropical Africa are important regions for the most primitive endemics since nine of the twenty-six endemics found in those two regions are classed as primitive-A. Thus, at the western and southwestern extremes of distribution for *Crepis*, we find the greatest concentration of the most primitive endemics in the genus.

In order to give another picture of the morphological contrasts between these most primitive endemics and the most advanced endemics in the genus, *C. terglouensis*, an alpine species found only in the European Alps, is shown in fig. 4, a-f, and *C. fuliginosa*, a lower montane species of southern Greece, in fig. 4, a'-f'. The plants and their parts are all drawn at comparable scales. It will be noted that, in their haploid sets of chromosomes, the two species represent the extremes of variation found in *Crepis* in both number and size of the chromosomes.

With further reference to the chromosomes of fifty-three of the endemic species (Table 5), it is clear that the 6-paired endemics are restricted to regions I to IV except for one species, *C. kashmirica*, of northwestern India. In fact



TABLE 5

RELATIONS BETWEEN THE ENDEMIC REGIONS FOR *Crepis* AND THE PHYLOGENETIC GROUP, ALTITUDE AND DURATION OF LIFE OF 133 ENDEMIC SPECIES; AND THE HAPLOID OR BASIC CHROMOSOME NUMBERS OF 53 OF THE SAME SPECIES

Endemic regions	Totals	Phylogenetic groups				Altitude classes			Duration classes		Chromosome numbers				
		Primitive		Inter- mediate	Ad- vanced	Alpine	Mon- tane	Low	Peren- nial	Annual or biennial	6	5	4	3	Totals
		A	B												
I. S. W. Europe; Alps; N. W. Morocco (mountains).....	8	3	2	3	..	3	3	2	8	..	2	1	3	..	6
II. Balkan Peninsula.....	26	2	3	14	7	6	13	7	19	7	4	3	6	1	14
III. Asia Minor; Syria-Palestine; Crimea.....	18	..	..	10	8	6	3	9	10	8	1	1	6	..	8
IV. Caucasus; Iran.....	13	..	5	8	..	5	5	3	13	..	1	1	..	..	2
V. Turkestan—Pamir-Altai region.....	6	..	3	3	..	3	3	..	6	..	..	..	1	..	1
VI. N. W. India.....	3	1	..	1	1	2	1	..	2	1	1	1	..	..	2
VII. S. E. Asia.....	9	..	..	9	..	1	8	..	9	..	..	..	..	..	..
VIII. E. Siberia.....	1	..	..	1	..	..	1	..	1	..	..	..	..	..	..
IX. Japan.....	2	1	..	1	..	2	..	..	2	..	..	..	2	..	2
X. Abyssinia; Eritrea; S. W. Arabia.....	8	..	2	3	3	2	6	..	6	2	..	1	..	..	1
XI. Africa (tropical and south)....	18	6	1	11	..	1	11	6	18	..	..	..	2	..	2
XII. Egypt to Morocco (littoral); Madeira and Canary Is.; S. Italy; S. France.....	21	..	..	11	10	..	2	19	14	7	..	2	13	..	15
Totals.....	133	29		75	29	31	56	46	108	25	9	10	33	1	53



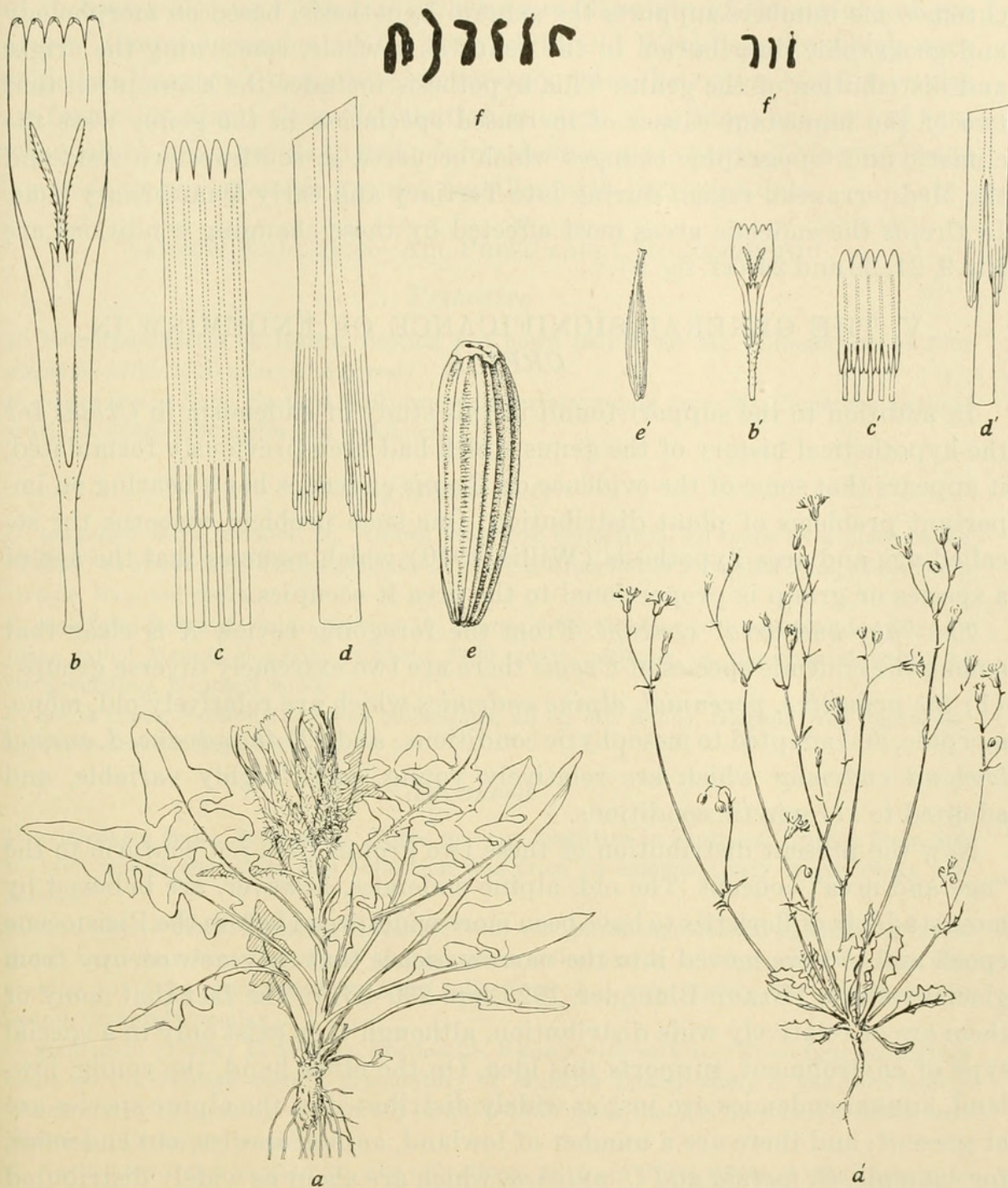


Fig. 4. *a-f*, *Crepis terglouensis* (Hacq.) A. Kern. *a*, plant,  $\times \frac{1}{2}$ ; *b*, floret lacking the ovary,  $\times 3$ ; *c*, anther-tube slit and opened out,  $\times 6$ ; *d*, detail of anther-appendages,  $\times 24$ ; *e*, achene,  $\times 6$ ; *f*, haploid set of chromosomes,  $\times 925$ . *a'-f'*, *Crepis fuliginosa* S. et S. all as above.

two-thirds of them occur in the mountains of southwestern Europe and the Balkan Peninsula. But the 5-paired endemics are widely distributed, and the 4-paired species still more widely, with a strong representation in the Mediterranean littoral. The evidence from chromosome numbers is consistent with the morphological evidence in showing that the oldest endemics are mostly in the mountains of southern Europe whereas the youngest endemics are mostly in the Mediterranean littoral and closely adjacent areas. This evidence from



chromosome numbers supports the general hypothesis, based on morphology and geographic distribution in the genus as a whole, concerning the origin and distribution of the genus. This hypothesis includes the assumption that two of the important causes of increased speciation in the genus were the climatic and topographic changes which occurred in southwestern Asia and the Mediterranean region during late Tertiary and early Quarternary time. In *Crepis* the endemic areas most affected by these changing conditions are 1 to 9, 21, 22 and 24 (cf. fig. 3).

## V. THE GENERAL SIGNIFICANCE OF ENDEMISM IN *CREPIS*

In addition to the support found in this study of endemism in *Crepis* for the hypothetical history of the genus which had been previously formulated, it appears that some of the evidence on *Crepis* endemics has a bearing on important problems of plant distribution. One such problem concerns the so-called age and area hypothesis (Willis, 1940) which assumes that the age of a species or group is proportional to the area it occupies.

*The "age and area" concept.* From the foregoing review it is clear that among the endemic species of *Crepis* there are two extremely diverse groups: (1) *the primitive, perennial, alpine endemics* which are relatively old, monomorphic, and adapted to mesophytic conditions; and (2) *the advanced, annual lowland endemics* which are relatively young, more highly variable, and adapted to xerophytic conditions.

Now the present distribution of these two groups does not conform to the "age and area" concept. The old, alpine endemics, however, are believed by most students of floristics to have been more widespread before the Pleistocene epoch and to have moved into the narrow niches that they now occupy from glacial refugia (Braun-Blanquet, 1923, pp. 260-261). The fact that many of them are of relatively wide distribution, although they exist only in a special type of environment, supports this idea. On the other hand, the young, lowland, annual endemics are just as widely distributed as the alpine species are at present; and there are a number of lowland, annual species, not endemics, for example, *C. foetida* and *C. pulchra*, which are about as widely distributed as the forerunners of the alpine endemics ever could have been. Hence the "age and area" concept breaks down completely with respect to these two groups of endemic species. As has been pointed out by Stebbins (1942) the concepts of "senescence" and "competition" are no more satisfactory than "age and area" in attempting to account for such diverse groups of species. But the concept that the monomorphic, alpine species are genetically homogeneous whereas the variable lowland species are genetically heterogeneous, i.e., composed of several or many biotypes, provides an acceptable explanation of their differences in variability and distribution.

*The nature of the "narrow" Crepis endemics.* This genetic approach to the problem of the differences between the widely distributed alpine and low-



land endemics also provides a satisfactory explanation of the nature of the "narrow" *Crepis* endemics. Of the forty-eight Old World species which were classified as "narrow" many are known only from their type locality or else the information about their distribution is vague; but there are several concerning which it is possible to make fairly definite statements. These are listed below in their phylogenetic groups, together with pertinent data.

#### NARROW ENDEMICS—ALL PRESUMABLY MONOMORPHIC

##### *Primitive*

1. *C. kilimandscharica* O. Hoffm. Section 8. Known only from Mt. Kilimanjaro at four stations, 2700–3500 meters, in forest.
2. *C. cameroonica* Bab. Section 8. Known with certainty only from Mt. Cameroon at three stations, 2000–4000 meters, in meadows.

##### *Intermediate*

3. *C. taygetica* Bab. Section 10. Known from five collections, all made at a place called "Porta" at about 2300 meters altitude on Mt. St. Elias in the Taygetus Mts., of southern Greece. Exposed rocks.
4. *C. crocifolia* Boiss. et Heldr. Section 10. Known from three or four collections made at a place called Megala Zonaria, at about 2400 meters altitude, on the same mountain as the preceding. Exposed rocks.
5. *C. athoa* Boiss. Section 10. Seven collections, all on Mt. Athos, Hagion Oros Peninsula, northern Greece. Exposed rocks.

##### *Advanced*

6. *C. eritreënsis* Bab. Section 20. Three or four localities in southern Eritrea from 800 to 1400 meters elevation. One collection was from "a comparatively moist, rocky formation."
7. *C. tybakiensis* Vierh. Section 20. Known from one specimen, collected in southern Crete. Since Crete has been botanized by numerous collectors, it is very probable that this species would be represented by more collections if it were widely distributed on the island. Certainly insular.
8. *C. divaricata* (Lowe) F. Schultz. Section 25. Known with certainty from four collections made on the isolated eastern promontory of Madeira Island where it has been nearly exterminated by grazing. (Reported in 1837–1850 from the tiny Desertas Islands near Madeira.) Certainly insular.
9. *C. Noronhaea* Bab. Section 25. Six collections, all from Porto Santo, a small island in the Madeira Archipelago. Certainly insular.
10. *C. Forskalii* Bab. Section 27. Two localities in Yemen Province, southwestern Arabia, between 1300 and 2500 meters elevation, in the coffee belt.

It is noteworthy that three of these species, *C. divaricata*, *C. Noronhaea* and *C. tybakiensis*, are insular and of very restricted distribution. However, they are relatively advanced species. Therefore their morphological homogeneity (assuming that *C. tybakiensis* is actually monomorphic) must be due to genetic homogeneity rather than to senescence. Five others in the above list, *C. kilimandscharica*, *C. cameroonica*, *C. taygetica*, *C. crocifolia* and *C. athoa*, are each found on only a single mountain. They are almost certainly "depleted" species (Stebbins, 1942) and they probably became isolated through widespread



changes in topography and climate during late Tertiary and Pleistocene times. In these also the population must be relatively small and homogeneous. The other two species may also be "depleted" species, although it must be admitted that the available information on their distribution and variability is scanty.

### SUMMARY

1. The twelve endemic regions for *Crepis*, comprising twenty-five areas, define the east-west distribution of the genus almost completely.

2. Seventy-two per cent of the Old World *Crepis* species are endemic in the sense that they are restricted to a single subcontinental geographic area. Among these endemic species are two very diverse groups, namely the most primitive, perennial species, half of which are alpine relics, and the advanced, annual species, most of which occur at low altitudes under arid conditions. The remaining endemics comprise an intermediate series connecting these two extremes. But comparatively few of the alpine perennials and of the lowland annuals have narrow distributions, i.e., their distributional areas, as at present known, are mostly over 150 kilometers in extent. From this evidence it is inferred that the alpine relics were formerly of wider distribution and that they moved into their present niches from glacial refugia; whereas the lowland, annual endemics have become adapted to a more arid climate but under conditions favoring genetic heterogeneity. From the evidence on morphology and distribution as well as on chromosome numbers it is inferred that the process of adaptation from mesophytic to xerophytic conditions went on in the genus as a whole over a long period of time.

3. The distribution of the most primitive and most advanced endemic species of *Crepis* supports the conclusion, derived from the evidence on phylogeny and distribution of the genus as a whole, that the center of origin was in Central Asia.

4. The "age and area" concept of Willis breaks down completely in the light of the evidence on the two diverse groups of endemic species mentioned above.

5. The concept of "senescence" fails to explain the existence of narrow endemics in *Crepis* since this group includes some of the most primitive and most advanced species in the genus. Since they are either insular or terrestrial, "depleted" species, the population is more or less restricted in size and relatively homogeneous.



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