CHROMOSOMES AND PHYLOGENY IN CREPIS

II. THE RELATIONSHIPS OF ONE HUNDRED EIGHT SPECIES

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INTRODUCTION

THE FIRST PAPER of this series (Hollingshead and Babcock, 1930), presented data on the number and morphology of the chromosomes in sixty-seven species of *Crepis* and three other species belonging in closely related genera. Since then it has been possible to study the chromosomes of fifty additional species and subspecies, and it is now possible to discuss the bearing of all these chromosome studies on the phylogenetic relationships of about half the species in the genus.

Our conception of the fundamental principles of biological classification remains essentially as set forth in the contribution cited. More recently one of us (Babcock, 1931) has discussed the species-concept and emphasized the value of chromosome number and morphology as one criterion of classification according to natural relationship. In *Crepis* this criterion has proved especially valuable. The genus is large and much diversified, many species are rare or little known, and from comparative morphology of the plants alone it is often difficult to draw definite conclusions. From a comparative study of the chromosomes it is sometimes possible to obtain the first clue concerning the manner of origin of certain species, and such clues have led to the discovery of confirmatory evidence from other criteria.

CYTOLOGICAL MATERIAL AND METHODS

Chromosomes are notoriously variable in appearance, even within a single individual, according to the conditions under which they are studied. Due precautions have therefore been observed for the study of comparable material. As in our earlier work and in most of the other researches in this field, the appearance of the chromosomes at mitotic metaphase has been used. Considerable refinement in the technique of comparing size and shape of the chromosomes has been attained by making camera lucida drawings of the best available diploid groups, identifying the several pairs present in the group, and deriving therefrom the members of the haploid genom. The illustrations in the present paper depict these haploid genoms all drawn to the same scale.

TABLE 1

CHROMOSOME NUMBERS IN FIFTY-FIVE SPECIES, SUBSPECIES, AND FORMS NOT PREVIOUSLY REPORTED

CREPIS—OLD WORLD

Species	Somatic chromosome number	Number of plants examined	Accession	Subgenus
**C. albida asturica* (Lacaita et Pau)	10	3	2088	B
C. albida macrocephala (Willk.)	10	2	2957	B
C. alpestris (Jacq.) Tausch	8	2	2512	C
C. argolica Babc	8	2	2884	E
C. argolica tirynica Babc	8	3	3036	E
C. aspera jordanensis Babc.	8	3	3010	B
C. aurea lucida (Ten.)	10	2	2912	C
C. bellidifolia Loisel	8	1	2921	B
C. bhotanica Hutchinson	16	2	3216, 3245	C
C. bifida (Vis.) F. et M.	10	6	3057, 3083, 3084, 3087	E
C. bithynica Boiss	10	3	3218	E
C. canariensis (Sch. Bip.)	8	3	3049	B
C. clausonis Pomel	8	4	2848	B
†*C. crocca* (Lam.)	16	6	2174, 2352, 2353	C
C. divaricata (Lowe) F. Schultz	8	4	2980	B
C. eigiana Babc	8	4	3125, 3138	E
C. critrcënsis Babc	10	1	3005	B
C. flexuosa (DC.) Benth. et Hook. f.	14	2	2983	E
C. fontiana Babc	8	3	3225	B
C. fuliginosa S. et S.	6	11	2994, 3043, 2891	E
C. granatensis Babc	8	4	1894	E
‡*C. hieracioides* Lowe	8	5	2817, 2818, 2823	B
C. hycmalis (Biv.) C. P. et G.	8	3	3053	B
C. hypochaeridea rhodesica Babc	8	1	3059	C
¶*C. juvenalis* (Delile) F. Sch.	8	7	3205, 3206, 3207	B
C. kashmirica Babc	12	4	3186	C
C. multicaulis congesta (Rgl.)	10	3	3187	E
C. mungieri Boiss	12	9	2870, 2876, 2877	E
C. myriocephala Coss. et DR. 4*n* forms	16	6	2844, 2845	B
C. nigricans Viv	8	3	3020	B
C. oreades Schrenk	8	1	2981	E

* Cf. *C. asturica* (Hollingshead and Babcock, 1930).
† Cf. *C. bungei* 2174 (Hollingshead and Babcock, 1930).
‡ One triploid plant.
¶ One trisomic.

TABLE 1—(*Concluded*)

Species	Somatic chromosome number	Number of plants examined	Accession	Subgenus
C. patula Poiret	8	2	2839	E
‖*C. polytricha* Turcz.	16	3	2562	C
C. pterothecoides Boiss.	8	3	3232	E
C. pumila (Lowe)	8	2	3022	B
C. pygmaea L.	12	1	3251	E
C. raulinii Boiss.	10	3	2875	E
C. reuteriana fa. *hirta* Babc.	8	2	3134	E
C. robertioides Boiss.	8	2	3129	E
C. sancta beirutica Babc.	10	3	3160	E
C. setosa topaliana Babc.	8	3	2906	B
C. stojanovii T. Georg.	8	2	3176	E
C. suberostris Batt.	10	1	2829	B
C. suffreniana (DC.) Lloyd	8	3	2975	B
C. taraxacifolia laciniata (Lowe)	8	3	2803, 2815, 2819	B
C. taraxacoides Desf.	16	2	2944	B
C. taygetica Babc.	40	3	2893	E
C. thomsonii Babc.	10	1	3208	B
C. triasii (Camb.) Fries	8	2	2945, 2949	B
C. tubaeformis Halacsy	8	3	3066, 3069	E
C. vesicaria L. 4*n* forms	16	3	2851, 2852, 2853, 2854, 2947, 2948, 3056, 3203	B
C. viscidula Froel.	12	3	3178	C
C. willemetioides Boiss.	12	3	3217	E
CREPIS—AMERICAN				
C. atribarba A. A. Heller	88?	2	3045	E
OTHER GENERA				
Lactuca depressa (Hook. f. et Thom.) (*Crepis depressa*)	16	1	3246	
Prenanthes glomerata Dcne. (*Crepis glomerata* Benth. et Hook. f.)	16	1	3252	

‖ Cf. *C. polytricha* (Babcock and Navashin, 1930).

Root-tips for this study were fixed in chrom-acetic-formalin solution 1, as described on page 3, Hollingshead and Babcock (1930). Paraffin sections were cut from 8 to 12μ thick and stained either in Heidenhain's iron haematoxylin or crystal violet. A Zeiss 1.3 oil immersion objective and Zeiss compensating ocular were used throughout this study. Drawings were made with a camera lucida at a magnification of 3750 and reduced to 2500 in reproduction. In all other respects a procedure was adopted which would produce results comparable with those reported by Hollingshead and Babcock (1930).

CHROMOSOME NUMBERS

The chromosome numbers of sixty-eight species of *Crepis* have already been reported. In table 1 are given the diploid numbers of forty species, nine subspecies, and several forms not previously reported. One subspecies is relisted because of a change in nomenclature; and one species (*polytricha*) appears here because it was not reported in the first paper of this series. The species commonly known as *Crepis glomerata* was excluded from *Crepis* by Babcock and Navashin (1930). This species has been referred to *Prenanthes*, where it was originally classified by its author. Another species, long known as *Crepis depressa*, has been referred to *Lactuca*. These two excluded species are listed at the end of table 1 for purposes of record. Classification of the *Crepis* species according to subgenus is shown in table 1, right-hand column; C = *Catonia*, E = *Eucrepis*, B = *Barkhausia*.

CHROMOSOME NUMBER AND PHYLOGENY

The Subgenera

In earlier publications four subgenera have been recognized, namely, *Paleya, Catonia, Eucrepis,* and *Barkhausia*. More recent studies show that the four species previously classified in *Paleya* are primitive representatives of *Catonia* and *Barkhausia*, therefore the subgenus *Paleya* has been merged with the two just mentioned. This makes possible a more satisfactory representation of phylogenetic relations.

In order to discuss the bearing of chromosome number on phylogeny, it is necessary first to consider the relationships of the three subgenera as determined from other evidence. It is not proposed to present all this evidence in detail here but merely to indicate the general situation as clearly as possible. In addition to the number of species in each subgenus, their duration of life (whether perennials or annuals and biennials), and their geographic distribution, certain aspects of their comparative morphology have been found especially valuable. The morphological characters used in differentiating the subgenera are presented most readily in the form of an analytical key.

KEY TO THE SUBGENERA

Bracts of the mature involucre unchanged or merely indurate.....*Catonia*
Bracts of the mature involucre dorsally keeled or spongy-thickened or both.
  Achenes unbeaked or only very shortly or coarsely beaked (rarely with beak equal to body).....*Eucrepis*
  Achenes definitely beaked; the beak usually long and slender.....*Barkhausia*

Without going into details or pausing to discuss certain exceptional species which are difficult to classify according to the foregoing scheme, it is obvious that there is progressive specialization in the structure of both involucral bracts and achenes. Along with this increasing specialization there is a definite trend toward reduction in length of life. Thus, all *Catonia* species are perennial; while one-fourth of the *Eucrepis* and three-fourths of the *Barkhausia* species are annual. The evidence from

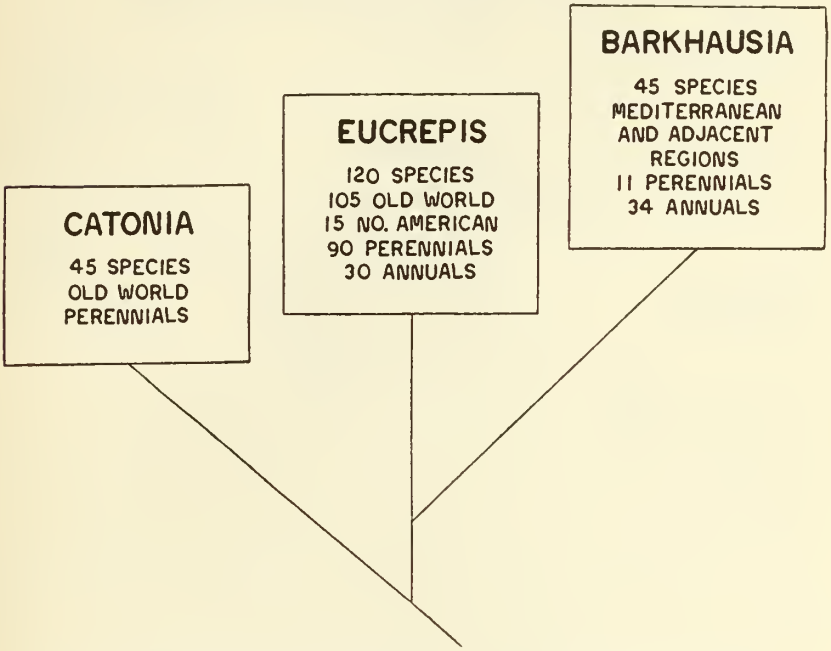

Fig. 1. Composition and phylogenetic status of the subgenera of *Crepis*.

geographic distribution will not be presented here; in general it is in agreement with the inference that *Catonia* is the most primitive, and *Barkhausia* the most recent group, while *Eucrepis* is intermediate. Furthermore, there are a number of border-line species in *Eucrepis,* some of which verge toward *Catonia* and others toward *Barkhausia.* Thus, the general situation in respect to phylogenetic relations between the subgenera may be represented as in figure 1.

Chromosome numbers in the subgenera.—The distribution of chromosome numbers in the three subgenera is shown in figure 2. An exponent indicates the number of species having a given chromosome number. This representation reveals several significant facts. It will be noted that the entire series of chromosome numbers is found in *Eucrepis,* while *Catonia* and *Barkhausia* have comparatively small series. But in each subgenus, as here represented, there is more than one basic number.

The basic numbers common to all three subgenera are 8 and 10, there being fifty-five species with eight, and nineteen species with ten chromosomes. In *Catonia* and *Eucrepis* there is a third basic number, namely, 12, and in *Eucrepis,* a fourth, namely, 14. But as will be shown, these "basic" numbers are not all equally primitive. Furthermore, the subgenera may contain more than one phylogenetic line of a given basic number.

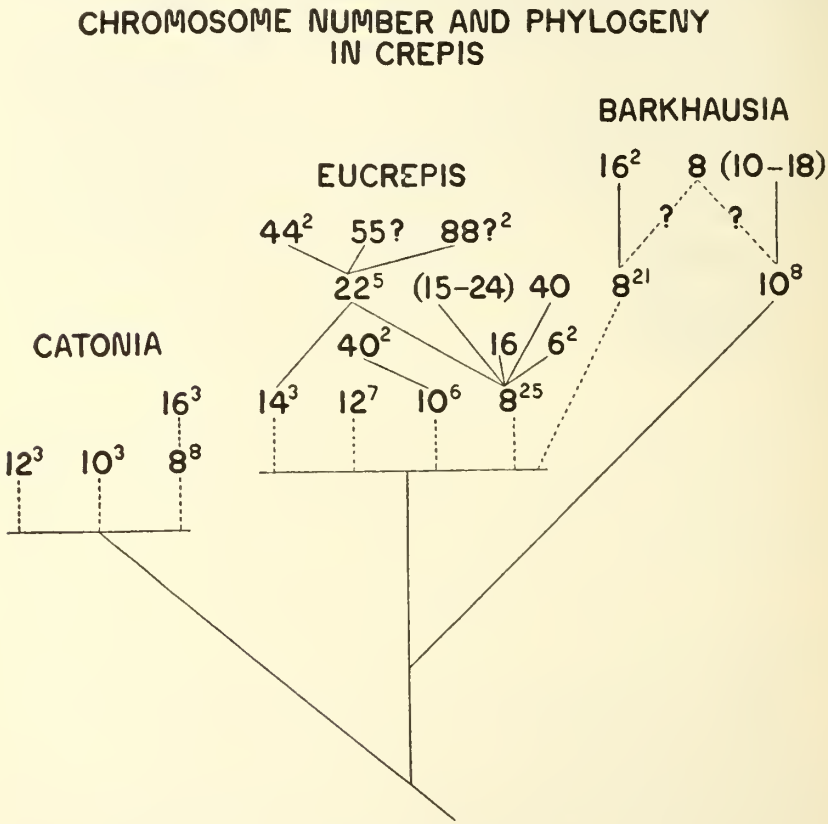

Fig. 2. Distribution of chromosome numbers in the subgenera in relation to phylogeny.

The great predominance of 8-chromosome species has led to the erroneous assumption by some writers that eight is the most primitive number in *Crepis.* But frequency of occurrence is not a sufficient basis for such an inference. The important fact that some of the 8-chromosome species are more highly specialized than any 10-chromosome species has been overlooked. Of still greater significance is the fact that none of the 8-chromosome species, even in *Catonia,* are as primitive in morphological aspects as are some of the 10-chromosome species, such as *sibirica* and *pontana* in *Catonia, raulini* and *bithynica* in *Eucrepis,* and *albida*

in *Barkhausia.* The 12- and 14-chromosome species present special problems which will be considered later. As between 8 and 10 the latter must be considered the more primitive number in *Crepis* or the progenitors of *Crepis;* but in the present representation 8, 10, 12, and 14 are all treated as basic numbers.

The diagram (fig. 2) also shows the comparative amount of differentiation in chromosome numbers in the three subgenera. In *Catonia* all the species have basic numbers except three, two of which certainly, and the third (*bhotanica*) probably, were derived from 8-chromosome ancestors. Predominance of basic chromosome numbers in this subgenus is associated with persistence of primitive morphological features. In *Barkhausia,* however, we have the most highly specialized portion of the genus. Yet all but three of the species thus far studied have the basic number 8 or 10. This immediately suggests the inference that the higher degree of specialization which is characteristic of *Barkhausia* has developed chiefly through other evolutionary processes than those involving changes in chromosome number. One such process, as has already been pointed out (Babcock and Navashin, 1930), is factor or point mutation (genovariation).

The greatest diversity in chromosome numbers occurs in *Eucrepis* and several different processes of alteration in chromosome number have been involved. From species with eight chromosomes there have been derived species with six by loss of one pair; species with sixteen by autotetraploidy; a species with fifteen, twenty, and twenty-four which seems to have arisen through amphidiploidy; polyploids with about forty. Species with eight and fourteen chromosomes respectively are believed to have hybridized and produced amphidiploids with twenty-two; and a polyploid series has been derived from the last. At the same time there are various degrees of specialization which may have been made possible largely by gene mutations.

Catonia

The phylogenetic relations of seventeen species of *Catonia,* as determined primarily from gross morphology, geographic distribution and chromosome number, are shown in figure 3. It must be admitted that the evidence from chromosome morphology, to be presented below, has also been considered in arranging this diagram; also the indications of relationship to be found in natural and artificial hybrids between species. In *C. blattarioides,* for example, gross morphology alone seems to connect it more closely with *sibirica* and *pontana* than with *alpestris* and *hypochaeridea,* but the evidence from chromosome number and morphology and the occurrence of natural hybrids between *blattarioides* and *alpestris,* seem to outweigh the evidence from superficial appearance. In

general, however, the degree of morphological resemblance is roughly indicated by this diagram.

The 5-paired species, especially *sibirica* and *pontana,* are in several respects among the most primitive morphological types in the entire genus, while *aurea,* particularly subsp. *lucida,* exhibits the greatest re-

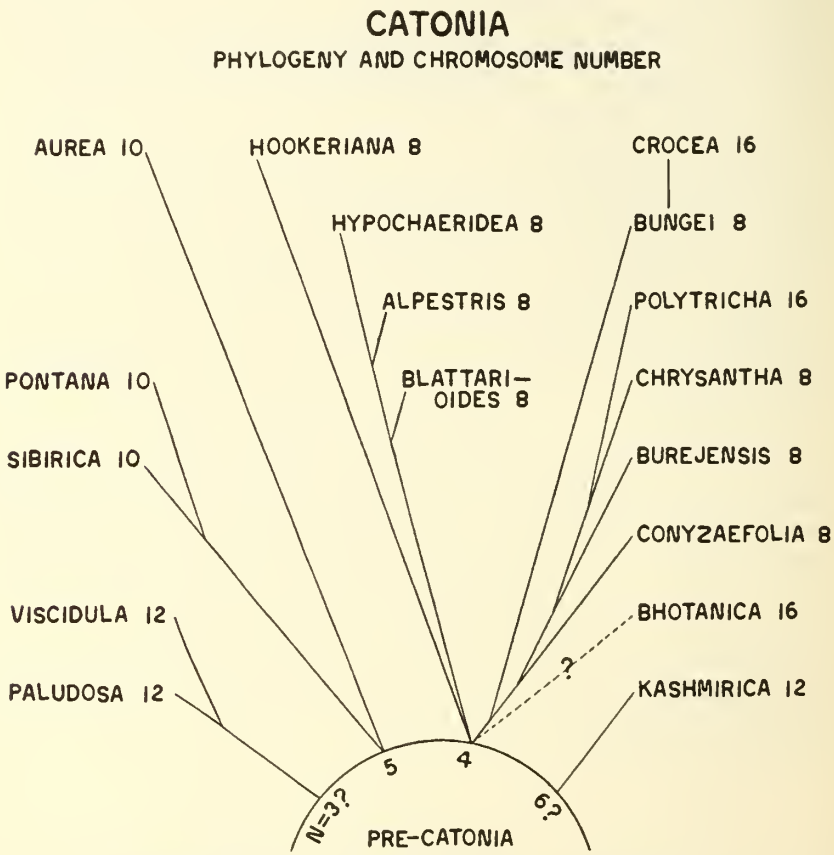

Fig. 3. Phylogenetic relations and chromosome numbers of seventeen species in subgenus *Catonia.*

duction in size of the whole plant and all its parts to be found in the *Catonia* species thus far studied cytologically.

The 4-paired *Catonia* species fall into two main groups and they may represent two or three different progenial stocks. On the left are shown the three species already mentioned and *C. hookeriana,* which is sufficiently like *hypochaeridea* to suggest that it diverged from the same stock. On the right are six species, *conyzaefolia-crocea,* which are evidently related and which may have sprung from the same stock as the 4-paired species on the left. The evidence for derivation of *crocea* from

bungei will be given below. Both *crocea* and *polytricha* are certainly polyploids with $n = 4$ as the base number. *C. bhotanica* is a prominent species with sixteen chromosomes, which shows sufficient resemblance to those just above it in the diagram to warrant the assumption that it arose from the same 4-paired ancestral line; but our study of chromosome morphology has not gone far enough to demonstrate conclusively that it is a polyploid with $n = 4$ as the base number.

The 12-chromosome *Catonia* species certainly represent two widely divergent lines, which differ greatly from each other morphologically as well as from all other species in the genus. On the extreme left are *paludosa* and *viscidula* which, in habit and fruit characters, show some resemblance to *Hieracium* species. Apparently they represent a rather stable primitive stock, because few if any other distinct species are known to belong in this group, although *paludosa* is one of the most widely distributed species in the genus. On the extreme right is *kashmirica,* which has long been confused with *blattarioides* although the resemblance is merely superficial. There is still some question whether these three 12-chromosome species are diploids or polyploids of some sort. The haploid number may be 3 or 6.

Eucrepis

Fifty-nine species of *Eucrepis* are arranged in figure 4 according to phylogeny and chromosome number. Here again chromosome morphology has been considered together with other available criteria of relationship; and the degree of resemblance in gross morphology is roughly indicated by the arrangement of groups and within groups. In general the more primitive species are below and the more specialized forms above, with the exception of the two perennials, *oreades* and *robertioides,* which appear above *biennis* and *ciliata,* and the ten American species which are placed at the top because they are probably of comparatively recent origin.

The species having 4 as the haploid number are all on the left side of the diagram except the *oreades-suffreniana* assemblage on the upper right. Of all the 8-chromosome *Eucrepis* species, *patula* is in certain respects the most primitive and it has no close relatives. But the *pannonica* series of perennials and the *argolica* group of annuals were probably derived from an ancestral stock represented by *patula,* which is apparently a relict in which certain parts, especially the pappus, have become very greatly reduced. *Pannonica, lacera,* and *chondrilloides* are closely related and fairly primitive species, while *incana* and *taygetica* are polyploids showing considerable resemblance to them. The *argolica* quartet is a very closely related group in which the marked differentiation in gross morphology must have come about through gene mutation.

On the other side of *patula* are *tenuifolia* and the *gymnopus-pterothecoides* group. Evidence that *tenuifolia* has 4 as the basic haploid number will be presented under chromosome morphology. This species is the

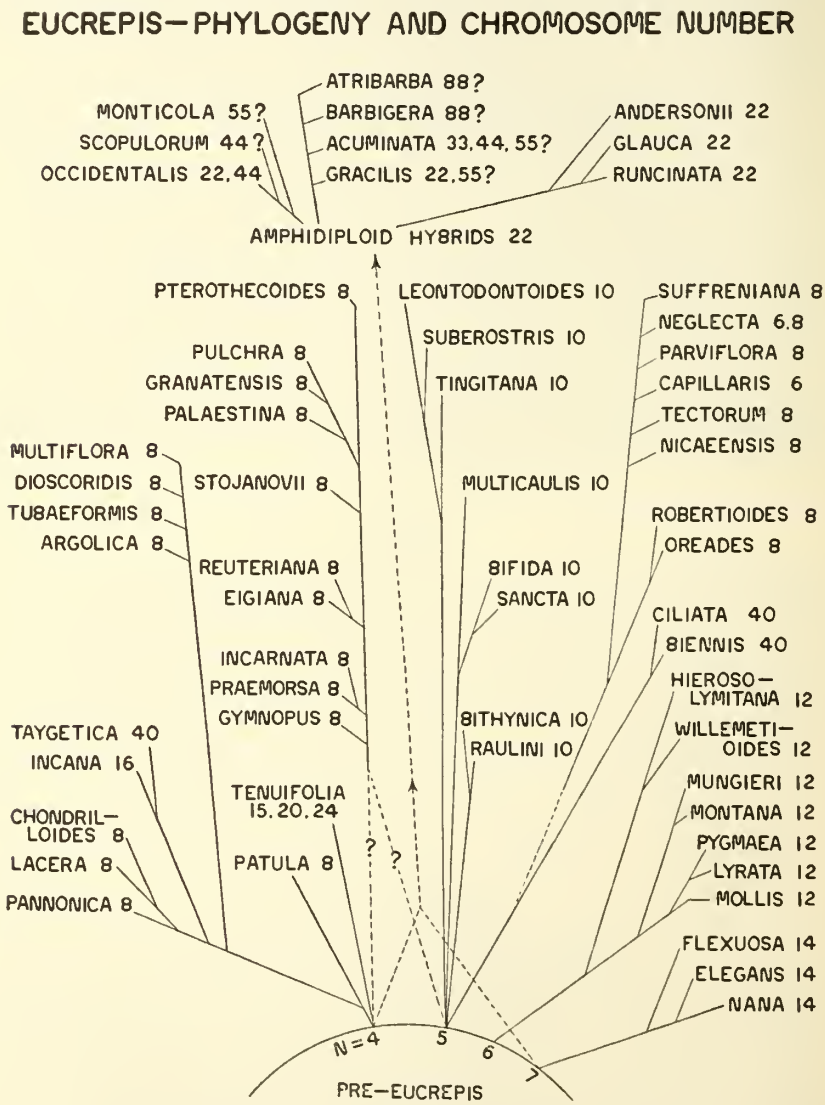

Fig. 4. Phylogenetic relations and chromosome numbers of fifty-nine species in subgenus *Eucrepis*.

only representative, thus far studied cytologically, of an eastern Asiatic group which was probably derived from a 4-paired stock different from the *patula* line. At any rate, that the two lines have diverged widely is

shown not only by gross morphology but also by geographic distribution, since the known representatives of the *patula* line are all restricted to the Mediterranean region.

The *gymnopus-pterothecoides* series is a remarkable group of related species in which reduction in life-cycle and morphological specialization has proceeded without change in chromosome number and without much change in chromosome morphology, as will be shown below. The lower five species in this series are perennials with relatively unspecialized fruits; while the upper five are annuals which are all more specialized, especially in fruit characters, than the perennials. The most extreme example of such specialization is found in *pterothecoides,* in which the achenes are shortly beaked and this plant, unlike all the others, is very precocious and short-lived. These ten species, therefore, provide a beautiful example of an evolutionary series in which, by elimination, it must be concluded that the genetic process making evolution possible is gene mutation. The problem of derivation of this interesting group, however, involves the possibility of transformation in chromosome number from 10 to 8. This will be discussed under chromosome morphology. For the present it is sufficient to indicate by the broken lines and question marks that the group may have come from either a 4-paired or a 5-paired progenial stock.

The *oreades-suffreniana* assemblage, with $n = 4$ for base number, as treated here, also involves hypothetical derivation from a stock with $n = 5$ as base number. This hypothesis is supported by two lines of evidence. First, *biennis* with about forty chromosomes has been proved by cytogenetic study (Collins and Mann, 1923) to be an octoploid species and its close relative, *ciliata,* has the same number of chromosomes. Second, *nicaeensis,* with eight chromosomes, is a biennial species and is so similar in general appearance to *biennis* as to make it difficult for anyone but an experienced student to identify herbarium specimens of the two species. The annual species, *tectorum,* also shows considerable resemblance to *nicaeensis* and *biennis,* and the other four annuals, *capillaris, parviflora, neglecta,* and *suffreniana,* are progressively farther removed. The alpine perennials, *oreades* and *robertioides,* each with eight chromosomes, are thought to be more primitive representatives of the same 4-paired stock that produced the *nicaeensis* group.

The 10-chromosome *Eucrepis* species appear in the central part of the diagram. Only eight such species have been reported thus far, but there are several related species which have not been available for cytologic study. These eight species comprise three diverse groups which probably represent different lines in the immediate ancestry although these lines converge and probably originated in a common progenial stock. The most primitive group contains *raulinii* and *bithynica,* which are alpine perennials with a woody caudex as in the 4-paired

species, *oreades* and *robertioides;* this fact gives added weight to the hypothesis that the latter originated from a 5-paired ancestral stock.

The *multicaulis* and *sancta-bifida* assemblage is extraordinarily interesting in that *sancta* and *bifida* represent a group of about ten species which have hitherto been classified under the genus *Pterotheca* although Hooker (1882) expressed the opinion that this group should be merged with *Crepis.* Since the one character supposed to distinguish *Pterotheca* from *Crepis* (bristle-like paleae on the receptacle) is sometimes absent, Hooker's opinion appears to be sound, and now that evidence both morphological and cytological establishes the relationship of these two species with *Crepis multicaulis* this opinion is confirmed. The question of relative position in the phylogenetic series is somewhat complicated. *Sancta* and *bifida,* because of their annual habit and dimorphic fruits, would be considered more specialized than *multicaulis;* but reduction in size of flowers and fruits has gone much farther in *multicaulis.* The position of these three species as represented in figure 4 is largely a matter of convenience.

Crepis tingitana, a native of Morocco and Spain, is in certain respects a primitive species. At any rate it shows strong resemblance to certain African species of *Catonia.* In shape of achenes, however, it is variable, certain forms having the achenes definitely though coarsely beaked. From external morphology alone it would seem unlikely that *tingitana* arose from the same 5-paired stock as the preceding species. At the same time it shows sufficient resemblance to *suberostris* and *leontodontoides* to warrant the inference that they may have arisen in the same ancestral line. But the two latter species are more highly specialized, particularly *suberostris,* which is an annual; while both include forms with *Barkhausia*-like achenes.

The seven 6-paired species comprise a well marked yet much diversified group. *C. mollis* is evidently the most primitive; then come *lyrata* and *pygmaea;* then the two pairs of closely related species, *montana* and *mungieri, willemetioides* and *hierosolymitana.* There are no closely related groups, so it appears that they arose from a distinct ancestral stock. But certain peculiarities in the morphology of their chromosomes remain to be considered.

The three 7-paired *Eucrepis* species, *nana, elegans,* and *flexuosa,* are also closely related to one another and seem to have arisen from a distinct ancestral stock. There are good reasons for thinking that these low-growing perennials are some of the remaining representatives of a comparatively ancient group. In fact, the most diminutive one, *C. nana,* is also the most widely distributed species in the entire genus, extending from central Asia across the northern hemisphere to northeastern North America. Such evidence as this lends support to the hypothesis which has been advanced (Hollingshead and Babcock, 1930) that 7-paired

species must have hybridized with certain 4-paired species and produced through amphidiploidy the 22-paired American species and their polyploid relatives shown at the top of figure 4 (cf. fig. 15*b*).

Barkhausia

The phylogenetic relations of thirty-two species of *Barkhausia* and their chromosome numbers are shown in figure 5. In general the most primi-

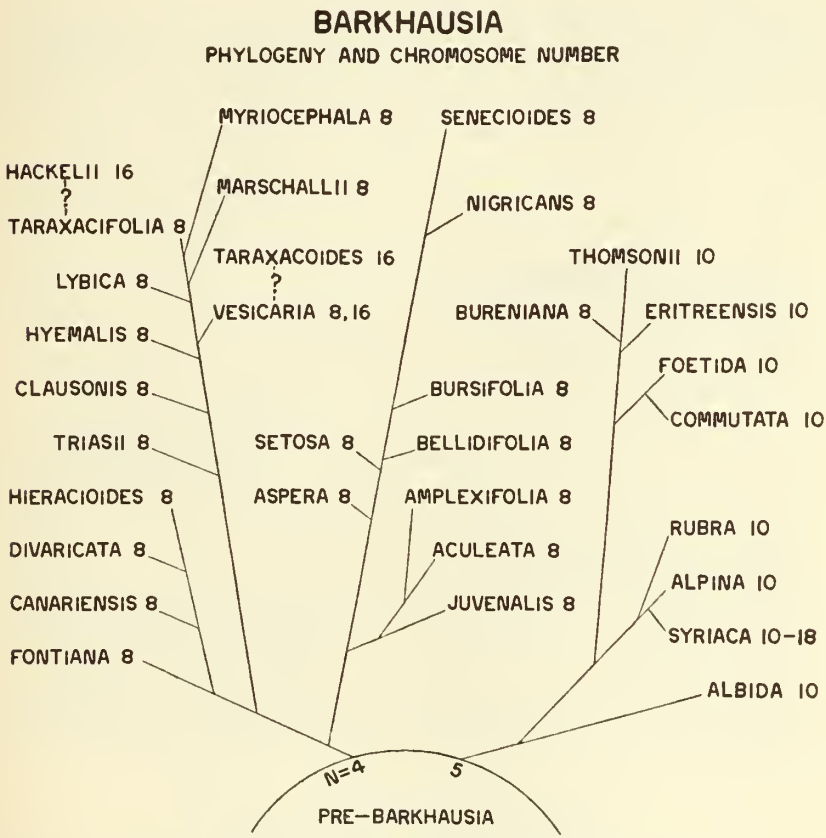

Fig. 5. Phylogenetic relations and chromosome numbers of thirty-two species in subgenus *Barkhausia*.

tive species are near the base and the most specialized at the top. The species having ten chromosomes, shown on the right, include one perennial, *C. albida*, of southwestern Europe and Morocco, which consists of six subspecies and which is one of the most primitive specific groups in the entire genus. There is good morphological evidence of its fairly close relationship to *C. alpina* of Asia Minor, and the associated species, *C. syriaca;* also, though less closely, to *C. rubra* of southern Europe;

while farther removed but still clearly connected is the *commutata-thomsonii* group of southern Europe, Asia Minor, northeast Africa, Persia, and India. Allied with the latter, especially with *C. thomsonii,* is the 8-chromosome species, *C. bureniana.* The morphological evidence of this relationship is indisputable. The question of chromosome morphology is discussed below.

The 8-chromosome *Barkhausia* species include three distinct series which seem to have a common origin. Below on the left are four perennial species, *fontiana* of western Morocco, *canariensis* of the Canary Islands, and *divaricata* and *hieracioides* of Madeira. They exhibit considerable morphological similarity. *Fontiana* and *canariensis* especially must be recognized as fairly primitive types of *Barkhausia.* Next to these is the *triasii-myriocephala* assemblage of the Mediterranean Islands and bordering countries. Of these, *triasii, clausonis, hyemalis,* and some forms of *vesicaria* are perennials, while the others are annuals which sometimes behave as perennials under favorable conditions. *C. myriocephala* is unquestionably the most specialized member of this series through reduction in size of flower heads, florets, and fruits, although the plant and its basal leaves are very large. The assumed derivation of *hackelii* from *taraxacifolia* and of *taraxacoides* from *vesicaria* is considered in connection with chromosome morphology.

The remaining series of 8-chromosome *Barkhausia* species, all of the Mediterranean littoral, are annuals except *bellidifolia* and *bursifolia,* which, although rather specialized through reduction in size of plant, flowers, and fruits, have retained the perennial habit. *C. juvenalis, aculeata,* and *amplexifolia* are obviously closely related, being characterized by having two distinct types of achenes which are similar in all three species. *C. aspera* and *C. setosa* also have dimorphic achenes, but they differ from each other and from the *juvenalis* group in important characters of the fruits. The two remaining species, *nigricans* and *senecioides,* are most highly specialized through reduction throughout the whole plant. They are very precocious, short-lived annuals.

CHROMOSOME MORPHOLOGY

The general aspects of chromosome morphology in *Crepis* have been discussed in earlier publications (cf. Hollingshead and Babcock, 1930; Babcock and Navashin, 1930). The existence of comparable pairs of chromosomes in different *Crepis* species was first noted by Navashin (1925) and designated as follows: A, long chromosome with longest proximal arm; B, long chromosome with next longest proximal arm; C, usually a shorter chromosome with shorter proximal arm, but sometimes there is little difference between B and C; D, satellite-bearing chromosome; E, a shorter chromosome with median constriction. In the

following illustrations the same order of arrangement of the members of the haploid genom has been followed throughout. This order, from left to right, is A, B, C, D, E, in 5-paired species. Diploid species with more than five pairs often have two or more pairs of E chromosomes, but sometimes B or C seems to be duplicated. The 4-paired species lack E; the 3-paired species, *capillaris,* lacks B; the other 3-paired species, *fuliginosa,* lacks C.

Catonia

Cytological studies have been completed on fifteen of the seventeen species represented in figure 3. The haploid genoms of the three 5-paired species and of two of the 6-paired species are shown in figure 6. In the

Fig. 6. Species of *Catonia* with $n = 5$ and 6.

former a fairly close resemblance between *sibirica* and *pontana* will be seen in all five chromosomes, the chief difference being in the length of the proximal arms of A and B. This close correspondence is in agreement with the morphological evidence that these species are among the most primitive of the genus, although distinct in many characters and occupying widely separated geographic areas. The genom of *aurea* differs strikingly, all the chromosomes being smaller and the C having a very short distal arm. *Aurea* is a more recent species, since it exhibits specialization through reduction in size and in the strongly attenuate achenes and the development of much red color in the flowers.

The two 6-paired species are of special interest for several reasons. They are closely similar, yet unquestionably distinct in numerous characters. *Paludosa* is the most widely distributed species of *Catonia,* while *viscidula* is restricted to the northern Balkan states. Furthermore, *paludosa* is more reminiscent of *Hieracium* in habit, habitat, achene shape, and the yellowish brittle pappus than any other species which has been studied cytologically. Yet the number, 12, has not yet been reported in *Hieracium.* These two species therefore appear as one of several small groups which may justifiably be included within *Crepis,* but which verge more or less definitely toward some other genus. Since 12 is not known to occur in *Hieracium* one may fairly question whether it must be looked upon as a primitive number in *Crepis.* Possibly these two 6-paired species were derived from some 5-paired stock. Further study is needed on these two species and on *kashmirica* in order to solve this problem.

The eight 4-paired species of *Catonia* fall naturally into two groups according to chromosome morphology, as is shown in figure 7, and by comparing this with figure 3 it will be seen that this grouping agrees with the arrangement according to morphology, geographic distribution, and the occurrence of natural hybrids. The close correspondence between the chromosomes of *blattarioides* and *alpestris* is the more remarkable in view of the marked morphological differences between these two montane species of southern Europe. *C. alpestris* also occurs in Asia Minor, which adds weight to the assumption that it had a common origin with *C. hypochaeridea* of South Africa. The *hypochaeridea* genom has a strong resemblance to that of *alpestris* and there is a general morphological resemblance between the two plants. The Moroccan *C. hookeriana,* a plant of the Grand Atlas Mountains, also resembles *C. alpestris,* though less closely than *hypochaeridea,* and its chromosomes differ more, especially B and C. From the size of the chromosomes it would appear that these four species are of approximately equal age. The slightly smaller size in *hypochaeridea* is in agreement with the evidence from geographic distribution that it is somewhat more recent than the other three.

Strong similarity in size and shape also appears in the genoms of *conyzaefolia,* a species distributed from southern Europe to central Asia, and of *burejensis* and *chrysantha* of eastern Asia. The three are similar morphologically, as are their genoms, but *burejensis* is slightly more specialized than *conyzaefolia,* and *chrysantha* is much more reduced throughout. *C. polytricha* has been confused with *C. chrysantha,* from which it is easily distinguished by the larger, ventricose involucre and yellow indumentum and by other characters. Critical study of the chromosomes of *polytricha* has been difficult because of limited material. From available evidence it appears almost certain that this species is

an autotetraploid, but the marked differences between *polytricha* and *chrysantha* in the A and D chromosomes indicate that if *polytricha* did originate from *chrysantha* through polyploidy, the event was not of recent occurrence. This is consistent with the morphological differences between the plants and the wide geographical distribution of *polytricha*.

Fig. 7. Species of *Catonia* with $n = 4$ and 8.

Genoms of *C. bungei* and *C. crocea* of *Catonia* are shown in figure 8 in comparison with that of *C. oreades* of *Eucrepis*. Morphologically, *C. crocea* is either intermediate between the two diploid species or exceeds them both in certain quantitative characters. The geographic distribution of the three species is in excellent agreement with the hypothesis that *crocea* originated as an amphidiploid hybrid between the other two. Genetic evidence is limited to data on some F_1 hybrids between *bungei*

and *crocea.* These hybrids were intermediate between the two species and exhibited a low degree of fertility. Chromosome morphology agrees fairly well with the foregoing hypothesis, although the chromosomes of *oreades* and *bungei* are too similar to make the evidence definite. In arranging the haploid genom of *crocea,* in each of the four sets of two chromosomes the one believed to correspond with *bungei* is shown on the

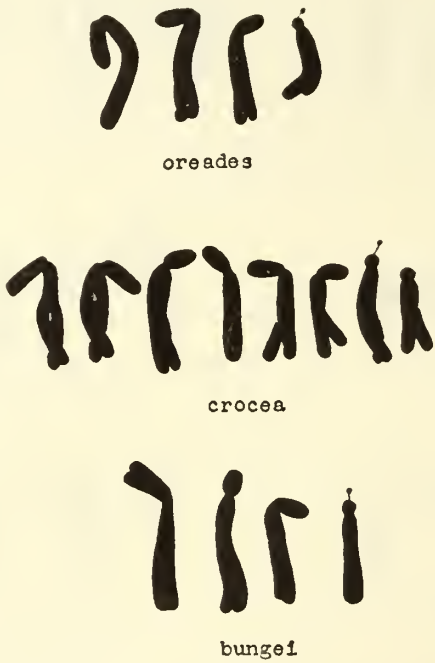

Fig. 8. Cytological evidence on the origin of *Crepis crocea.*

left. The absence of a satellite from the *"oreades"* D chromosome in *crocea* seems to be constant—another example of amphiplasty (Navashin, 1928).

Eucrepis

The genoms of the 10-chromosome *Eucrepis* species are presented in figure 9. It will be recalled that *raulinii* and *bithynica* are rather primitive types which may have arisen from the same 5-paired ancestral line as the other six species. The close correspondence in shape among all eight genoms agrees with this conception. The full significance of this evidence can hardly be appreciated without a somewhat detailed comparison of the morphology of the plants (pp. 297 f.). The high degree of reduction and specialization which has taken place in the *multicaulis* group seems to have been accompanied by notable reduction in size of the chromosomes. *Tingitana* also is a rather primitive species, while

leontodontoides is much more specialized in several characters. Here again there is notable difference in size of the chromosomes. *Suberostris,* however, seems an exception to the general rule since its chromosomes

Fig. 9. Species of *Eucrepis* with $n = 5$.

are large, although it is a considerably reduced annual. In fact it fits less well in this series than the other species, not only with reference to its chromosomes, but also in its external morphology; but it has no closer relatives.

Crepis patula and its nearest relatives are represented by the haploid groups of chromosomes shown in figure 10. That the relationship is not

Fig. 10. Species of *Eucrepis* with $n = 4$.

close is indicated by the fact that the *patula* genom does not correspond entirely with the chromosome types in either of the two series. It is noteworthy, however, that the B chromosome in *patula* corresponds with B

in the *argolica* series, while *patula* C is more like C in the *pannonica* series. This may indicate a common ancestry and is in keeping with the evidence that *patula* is really an old species which is still primitive in the greater number of characters but has become greatly reduced in a certain part. It is not unlikely that, in its comparatively long existence as a species, there has also been some reduction in the size of its chromosomes.

The close similarity of the *pannonica, lacera,* and *chondrilloides* genoms is to be expected from their common morphological features. It may be noted that *chondrilloides* is the most restricted in distribution and the most specialized of the three, and that its chromosomes appear to be slightly though perhaps not significantly smaller. That *incana* is an autotetraploid appears fairly certain from its B, C, and D chromosomes, and the apparent unlikeness in the A's may not be an actual difference. The diploid species from which it may have originated has not yet been discovered. *C. taygetica* may be mentioned here as another polyploid species, of which the diploid ancestor is unknown. Evidence from morphology and geographic distribution places it in this series. Incomplete study of its chromosomes indicates that it is a high polyploid of some sort, possibly a decaploid. The presence in somatic tissue of forty chromosomes which correspond in size to those of other species in this group lends considerable weight to this assumption. Only three chromosomes were observed which bore unmistakable satellites, but several others were present which might be D chromosomes and it is frequently found that, in a large genom such as this, all the D's do not possess a satellite. The *argolica* series of very closely related species from Greece also exhibit great uniformity in chromosome types. The only point of importance is the inconsistency with the general rule that more highly specialized and reduced species have smaller chromosomes, since *multiflora* is such a species, while *argolica* is certainly the most primitive of the four.

Crepis tenuifolia was reported by Hollingshead and Babcock (1930) as having fifteen chromosomes. This report was based on eight plants, grown from wild seed, of one accession from Mongolia. Since then we have counted the chromosomes of thirty-three plants, grown from wild seed, of a different accession also from Mongolia. Of these, thirty-one had fifteen chromosomes and two had twenty-four chromosomes as the diploid number. It appears that most Mongolian plants of this species have fifteen chromosomes, the odd number being maintained through some form of apomictic reproduction, but that sexual reproduction occasionally takes place, producing plants with higher numbers. More recently an accession of this species has been received from Kashmir, which has $2n = 20$. In figure 11*a* is shown a diploid group with fifteen chromosomes, and *b* is the haploid genom in which each of the eight

types represents a pair except the one at the right end, which is the odd member. It will be noted that there are two pairs of A's, B's, and D's in the diploid complex. Figure 11*c*, *d* presents the haploid genom of the Himalayan form of the species, in which each type shown in *c* represents a pair and the four chromosomes in *d* are odd. Referring to the haploid genom, there are certainly two types of D chromosomes and

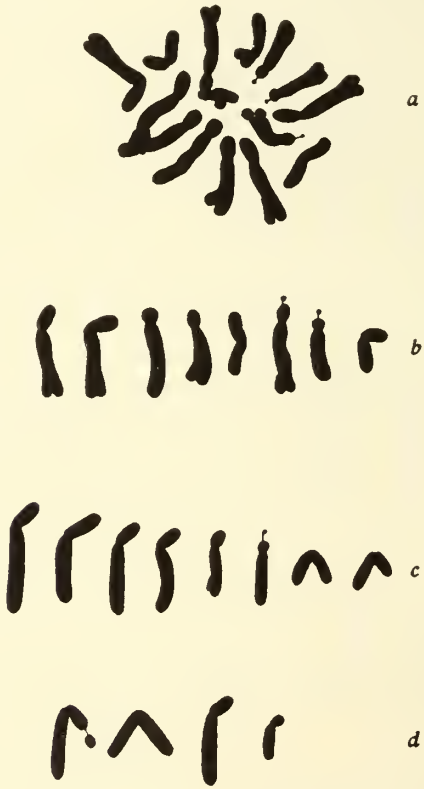

Fig. 11. *Crepis tenuifolia: a,* diploid genom of the 15-chromosome form; *b,* one member of each of the seven pairs in diploid genom and, at the right end, the odd chromosome; *c,* one member of each of the eight pairs in a 20-chromosome form; *d,* the four odd members in the same genom.

presumably also of A's, B's, and C's or E's. Hence it appears certain that the species originated as an amphidiploid hybrid and that the odd number, 15, is maintained by some form of apomictic reproduction, although sexual reproduction sometimes occurs producing such forms as the 24-chromosome plants already mentioned. The 20-chromosome form may also be a segregation product resulting from sexual reproduction. Further studies are in progress on this remarkable species.

In figure 12 are depicted the highly uniform genoms of the ten species in the *gymnopus-pterothecoides* series. The rather wide morphological

Fig. 12. Species of *Eucrepis* with $n = 4$.

differences among the members of this group must depend upon genic diversity. The extent of some of these differences is indicated from the fact that four of the species were originally classified and described under

three other genera, *Hieracium, Cymboseris,* and *Phaecasium.* Another was named for *Pterotheca* although the resemblance is only superficial. An interesting difference in chromosome morphology is the distal satellite on the C chromosome in *pulchra,* in its close relative, *granatensis,* and in *pterothecoides,* which resembles *pulchra* more than it does any other member of the series, although it is a distinct species. Since the preparation of this figure similar distal satellites have been discovered in *palaestina* and *reuteriana,* which are more closely related to *pulchra* than are the remaining species. The possibility that the genom characterizing this group was derived from some 5-paired ancestor has been mentioned. The suggestion comes from the fact that equiarmed A chromosomes are unique in *Crepis,* being found in only two other series (cf. figs. 14 and 15). If the putative ancestor had J-shaped A's and a pair of E's, it is conceivable that reciprocal translocation between A and E, followed by meiotic irregularities, might result in the V-shaped A chromosomes and elimination of the rest of the E chromosome, thus establishing this 4-paired type. Translocations between nonhomologous chromosomes, such as might lead to the origin of new chromosome numbers, have been observed in animals and plants, and Navashin (1932) has proposed a hypothesis of evolution of chromosome numbers based partly on the observation of such phenomena in *Crepis.*

The *oreades-suffreniana* series is represented in figure 13. There is fairly close correspondence between the genoms of *oreades* and *tectorum* and the two species occur in the same region of northern Asia. Although *robertioides* and *parviflora* are less similar in their haploid genoms, they both occur in Asia Minor and are probably distantly related. Both *oreades* and *robertioides* are woody-based perennials and in other respects also are more primitive than the other species in this series. Furthermore, *oreades* is much more primitive than *robertioides.* The other species are annuals (*nicaeensis* is often biennial) and progressive reduction in size of plant and parts reaches a climax in the low, delicate, short-lived forms of the *neglecta-suffreniana* group. Corresponding reduction in size of the chromosomes is very notable in this series. *Crepis capillaris* must now share its distinction as a 3-paired species with *fuliginosa.* In the latter it seems to be the C chromosome which is lacking, while in *capillaris* it is the B, but the distinction between B and C chromosomes is an arbitrary one. It may be significant, however, that the A and D chromosomes are present in both of these plants.

Crepis neglecta, sensu lato, presents a unique situation in respect to the chromosomes. In taxonomic treatments of this assemblage both *cretica* and *fuliginosa* have been classified in subspecific categories under *neglecta.* The morphological resemblances existing among the three entities are perhaps sufficient grounds for such a systematic treatment. In adopting it, however, it must be recognized that the divergence in chro-

mosome number, size, and shape is unusually great for a single species. With this frank admission there would seem to be no serious objection to such classification. For the cytological criterion is not of paramount

Fig. 13. Species of *Eucrepis* with $n = 4$ and 3.

importance: in spite of the differences in number and morphology of the chromosomes, essentially the same residual complement of genes may be present in all three entities. Critical comparison, however, reveals a num-

ber of significant morphological differences and these, together with the outstanding chromosomal differences, will justify recognition of the three as distinct, though very close, species. *C. suffreniana,* while closely related to *neglecta,* is beyond doubt a distinct species and its A and B chromosomes are notably different from those of *neglecta, fuliginosa,* and *cretica.*

Fig. 14. Species of *Eucrepis* with $n = 6$.

Preliminary study of the haploid genoms of *C. biennis* and *C. ciliata,* in both of which $2n = \pm 40$, indicates that they are certainly octoploids, based on $n = 5$, as has been previously reported for *C. biennis* (Collins and Mann, 1923). In both species there are two sizes of D chromosomes which may indicate hybrid origin. Further study is reported elsewhere (Babcock and Swezy, 1934).

Figure 14 shows the haploid genoms of the 6-paired *Eucrepis* species. The species are arranged in the same relative positions as shown in figure 4, these positions being determined on the basis of comparative

morphology, as summarized earlier, and geographic distribution. *C. mollis* extends from western Europe to middle Russia; *pygmaea* occurs only in the European Alps, *montana* only in Greece, and *mungieri* only in Crete; while *lyrata* is found in western Siberia, *willemetioides* in northeastern Persia, and *hierosolymitana* in Palestine, Syria, and Cyprus. The wide distribution of the series as a whole and of its most primitive member indicates relative antiquity, and necessitates the acceptance of 12 as a primitive number in *Eucrepis,* unless it be assumed that these species originated through hybridization between 5-paired species, followed by amphidiploidy and consequent transformation and elimination of certain chromosomes. This assumption is well supported by the following comparative classification of chromosome types in the haploid genoms of the seven species.

mollis 2 A (1 V, 1 compound), B, C, 2 D lacking satellite.
pygmaea 2 A (both V's, 1 with satellite), B, 2 C, E.
lyrata 3 A (1 V, 2 with satellite), 2 C, E.
montana 2 A (1 V), B with satellite, 2 C, E.
mungieri A, B, C?, D, 2 E.
willemetioides 2 A (1 V, 1 with satellite), B, C, 2 E.
hierosolymitana 2 A (1 V, 1 compound), B, C, D lacking satellite, E.

The foregoing classification is made by comparing each chromosome with the characteristic types in a basic 5-paired genom; it does not depend on the order of arrangement within the haploid groups shown in figure 14. The presence of E chromosomes in all but one of the seven species, the duplication of E, D, C, and A chromosomes, and the striking alterations of A chromosomes in most of these species, all strongly indicate hybrid origin and that the parental species involved had five pairs of chromosomes.

The genoms of the 7-paired *Eucrepis* species are shown in figure 15. The general similarity of the chromosome types is in agreement with the evidence from external morphology indicating that these are closely related species. But there are notable differences among the first three chromosomes from the right end of each haploid group. Like the 6-paired species this is a widely distributed and relatively ancient group, the members of which have become much reduced and considerably specialized concomitantly with their adaptation to the rigors of alpine and arctic environments. This seems to indicate that 14 is also a primitive number in *Crepis.* But here also it is not difficult to imagine that these species originated through hybridization of 5-paired species plus amphidiploidy, followed by transformation and elimination of some chromosomes. The presence of E chromosomes and more than one pair of certain chromosome types in all three species strongly supports this hypothesis. Two species are known from very high altitudes in the Himalaya Mountains. These might have been the parents of this group, but

unfortunately they have not been studied cytologically. Even if they should not have the proper chromosome number and morphology, however, this would not greatly discount the hypothesis here advanced. The possibility should also be noted that both putative parents were 4-paired species and that these 7-paired species are modified derivatives from a 16-chromosome amphidiploid. At any rate it is hardly justifiable to con-

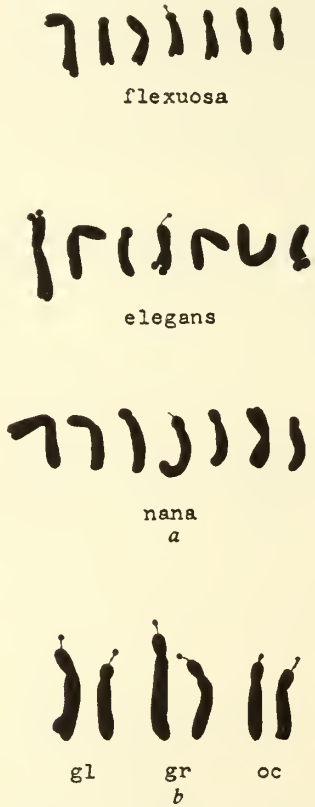

Fig. 15. *a*, Species of *Eucrepis*, with $n = 7$; *b*, representatives of the two pairs of D chromosomes of *glauca* (gl), *gracilis* (gr), and *occidentalis* (oc), indicating origin of all three groups of American species with $n = 11$ through interspecific hybridization and amphidiploidy.

clude that either 12 or 14 is a truly primitive number in *Eucrepis* until it is shown that the species under discussion could not have originated through interspecific hybridization and amphidiploidy.

Analysis of the distribution of chromosome types in the octoploid and decaploid species has not been attempted. In some of the 22-chromosome American species, however, there is definite cytological evidence indicating the manner of their origin. It is noteworthy that the number, 22, could not have arisen by autotetraploidy from any haploid number known in *Crepis*, although it is conceivable that autotetraploids with

twenty or twenty-four chromosomes might have produced 22-chromosome derivatives. But preliminary studies of the genoms of some 22-chromosome species indicate that they cannot be autotetraploids. This is most clearly demonstrated by comparison of the two pairs of satellite-bearing chromosomes found in each of these species. In figure 15*b* are shown representatives of the two pairs of D chromosomes from each of three species, *glauca, gracilis,* and *occidentalis,* representing the three subgroups of this assemblage. In *occidentalis* the difference is slight but in *glauca* and *gracilis* there are obvious differences in size of the two pairs. This evidence, together with 11 as the haploid number for ten species, is sufficient proof that all the American species except *nana* and *elegans* originated through hybridization of 8– and 14–chromosome species followed by amphidiploidy.

Barkhausia

The 10-chromosome *Barkhausia* species are compared with reference to their haploid genoms in figure 16. It will be recalled that *albida* is certainly the most primitive member of this series and that *alpina* is its nearest relative. The proximal arm is longer in the A and C chromosomes of *albida;* also the D and E chromosomes are larger in this species. *C. syriaca* is believed to have originated through hybridization of two *alpina* subspecies followed by genic mutation and chromosomal modification. Indigenous plants possess supernumerary chromosomes, mostly of one type, which is not shown here as part of the basic haploid genom for reasons advanced by Cameron (1934). The basic genom of *syriaca* resembles closely the haploid group of *alpina.* These two closely related species are natives of Asia Minor and the Caucasus while *rubra* occurs in Crete, the southern Balkans, and Italy. *C. rubra* must be considered a more recent species because of reduction in size of plant and especially because of its pink flowers as contrasted with the yellow flowers which occur in all other *Barkhausia* species. Furthermore, its scape-like flower stems point to some species other than *alpina* or *albida,* although this species doubtless arose from the same ancestral stock as the two latter. It is not surprising, therefore, to find some striking differences in chromosome morphology in *rubra,* but the larger size of its chromosomes makes it another illustration showing that reduction in size of the chromosomes does not always accompany higher development. The *commutata-thomsonii* series has a markedly uniform type of genom, as would be expected from the similar morphology of the four species. The genom of *C. bureniana* is included in figure 16 because, on morphological grounds, this species is certainly related to *foetida* or *thomsonii* and because, judging from geographical distribution, the latter is probably its closest relative. Its chromosomes, however, resemble those of *alpina* more than those of *thomsonii* although the genoms of the

two latter species are undoubtedly similar. This suggests several possible modes of origin for *C. bureniana*, but these are all too vague to justify further discussion here. An investigation of this species is in progress.

Fig. 16. Species of *Barkhausia* with $n = 5$ and 4.

In figure 17 are shown the genoms of two related *Barkhausia* series. The strong general resemblance of the genoms is the most striking thing in this illustration and from the external morphology of these species it seems certain that they all arose from the same ancestral stock. The lower four are the more western species, of which *fontiana* and *canariensis* are recognized as more primitive; and the chromosomes of *fontiana* are definitely larger than any of the others. Of the remaining nine spe-

Fig. 17. Species of *Barkhausia* with $n = 4$ and 8.

cies, the lower four are more primitive and their chromosomes are somewhat larger. *C. vesicaria, myriocephala, marschallii,* and *taraxacifolia* are very closely related and their chromosomes show the closest similarity. The *marschallii* genom is not illustrated. This species is most closely related to *taraxacifolia* and its chromosomes resemble those of that species closely, except the B, which is more like the B of *vesicaria.* That *C. taraxacoides* is an autotetraploid is clearly indicated by the virtual identity of its corresponding pairs of A, B, C, and D chromosomes; and they resemble those of *vesicaria* so nearly as to suggest this as the parent species. Furthermore, autotetraploid forms of *vesicaria* have been discovered (table 1) which resemble the typical diploid form rather closely except in size throughout. But *taraxacoides* differs from *vesicaria* in certain important characters, particularly in the involucre. Therefore, if *taraxacoides* did spring from *vesicaria* through autotetraploidy, it was not a recent event. In *hackelii* the A, B, and D chromosomes are sufficiently unlike to suggest origin through amphidiploidy with *taraxacifolia* as one parent. But no other species is known which, by its morphology and native habitat, could have been the other parent. Therefore, it seems more probable that *hackelii* also originated through autotetraploidy and that there has been some chromosomal alteration.

The remaining 4-paired *Barkhausia* species are represented in figure 18. There can be no doubt that *aculeata, juvenalis,* and *amplexifolia* are closely related species and that the last is the most highly specialized. Its chromosomes are much smaller than those of the other two. The C chromosome of *juvenalis,* however, is smaller than that of *aculeata,* yet *juvenalis* is less reduced in size of heads and achenes than *aculeata,* though in size of plant it is smaller. In comparing the chromosomes of *aspera* and *setosa* it may be noted that the "A" and "B" of *aspera* might well be interchanged; they would then compare fairly closely with the A and B of *setosa.* At any rate, the most striking differences in the two genoms are found in the C and D chromosomes. In size of heads and achenes *setosa* is more reduced than *aspera,* yet it has about the same total chromosome length. The genoms of the two perennial species are closely similar and they are probably about equal in age, although the fruits of *bursifolia* have become much more reduced and specialized, with a relatively long delicate beak, than those of *bellidifolia.* The same is true of *senecioides* and *nigricans* except that, in the former, reduction in size of fruits and specialization of the beak is even more extreme, and its chromosomes are definitely smaller. The notable difference in each of the four chromosomes is consistent with the morphological evidence that the two species are not closely related. In fact, from the achenes alone the closest relative of *senecioides* is *bursifolia* and the chromosomes of the two species are similar except in size.

Fig. 18. Species of *Barkhausia* with $n = 4$.

SUMMARY AND CONCLUSIONS

1. *The genus.*—*Crepis* is a natural group of more than two hundred species, distributed widely in the northern hemisphere and Africa. Some of them are common and well-known plants while many are extremely rare, little known, or occur only in relatively inaccessible places. In the past decade one hundred seven species of *Crepis* have been obtained in living condition from all parts of the world and examined cytologically. The present paper combines these cytological data with other evidence bearing on phylogenetic relationship.

2. *The subgenera.*—*Catonia* with about one-fourth, *Eucrepis* with about one-half, and *Barkhausia* with the other fourth of the species, are the major natural subdivisions of the genus. They are characterized in the order just given by progressively greater specialization of the involucre and fruits, and along with this differentiation goes generally reduction in length of life-cycle and in size of the plant and its parts.

3. *Chromosome numbers in Crepis.*—The series of characteristic diploid numbers found in the Old World species is 6, 8, 10, 12, 14, 16, 40, and in North American species 22, 33, 44, 55(?), 88(?), besides 14 in two representatives of an Old World group. Occasional irregularities in these characteristic numbers occur and several species are known to have variable numbers.

4. *Chromosome numbers in the subgenera.*—The number of species having a given chromosome number being indicated by an exponent, the distribution of chromosome numbers of Old World species is as follows: *Catonia*, 8^8, 10^3, 12^3, 16^3; *Eucrepis*, 6^2, 8^{25}, 10^6, 12^7, 14^3, $(15–24)^1$, 16^1, 40^3; *Barkhausia*, 8^{22}, 10^8, $(10–18)^1$, 16^2. The American species are all of *Eucrepis*.

5. *The primitive numbers.*—Although 8 is the most prevalent diploid number in the genus, 10 must be considered more primitive than 8 because (1) the most primitive species in the genus, such as *sibirica*, *pontana*, and *albida* have 10; (2) no species with ten chromosomes are as greatly reduced or specialized as some of the species with eight chromosomes. If the 8-chromosome lines were derived from 10-chromosome ancestors, the most likely process would be by reciprocal translocations between nonhomologous chromosomes, followed by meiotic irregularities leading to complete elimination of one pair of chromosomes. Such a process seems the most probable mode of origin of the 8-chromosome species, *C. bureniana*, and of the two 6-chromosome species, *capillaris* and *fuliginosa*.

6. *Ancient but doubtfully primitive numbers.*—In addition to 10 and 8, the numbers 12, 14, and 16 must be considered as possibly primitive in this genus. In *Catonia* there are three species with twelve chromosomes

which may be diploids, aneuploids, or polyploids; and there are three species with sixteen chromosomes, two of which are polyploids and one is still doubtful. In *Eucrepis* there are seven species with twelve, and three species with fourteen chromosomes. They are widely distributed and fairly primitive, yet it is possible that they are all polyploids of some sort. The one species with sixteen chromosomes is a tetraploid. In *Barkhausia* there are no species with twelve or fourteen and the two with sixteen chromosomes are tetraploids. In view of the small proportion of species having these numbers and the uncertainty that these species are simple diploids, the numbers 12, 14, and 16 cannot be accepted as primitive. At least they are not basic like 8 and 10.

7. *Secondary numbers and modes of derivation.*—Secondary numbers are 6, 12, 14, 15, 16, 22, other multiples of 11, and 40. Each of the two species with six chromosomes, *capillaris* and *fuliginosa,* was probably derived from a 4-paired ancestor. The most probable mode of origin of these 3-paired species has been described (cf. *primitive numbers*). It is conceivable that all the species with twelve and fourteen chromosomes were derived from amphidiploid hybrids. The constantly increasing evidence on the importance of amphidiploidy in the evolution of higher plants and the demonstration that it has played a definite rôle in *Crepis* lend support to this idea. All but one of the 16-chromosome species have been shown to be either autotetraploids or amphidiploids. The 22-chromosome species are the products of interspecific hybridization and amphidiploidy, and the higher-numbered American species are polyploids derived from them. One of the 40-chromosome species, *biennis,* is an octoploid ($n = 5$) and the closely related *ciliata* may be one also. The other 40-chromosome species, *taygetica,* is probably a decaploid ($n = 4$). Thus there are certainly two general processes by which new chromosome numbers have originated in *Crepis,* namely, by interspecific hybridization with amphidiploidy, and by polyploidy. It is also necessary to assume that some process, such as reciprocal translocation, has led to reduction in number from 10 to 8 and from 8 to 6. The change from 10 to 8 is of basic importance in the evolution of the genus.

8. *Chromosome number and phylogeny.*—Throughout the genus there is close correspondence between chromosome numbers and external morphology of the plants. The most primitive species have ten chromosomes but there are fairly primitive 8-chromosome types. In both 10-chromosome and 8-chromosome series there is abundant evidence of progressive development from the woody-based perennial types with large simple leaves, few large heads, large florets, and large, unspecialized fruits to the short-lived annual forms with small or dissected leaves, numerous small heads, small florets, and very small or highly specialized fruits. The basic, primitive number is 10 and there are three 5-paired phylogenetic lines, one in each subgenus. There is also sufficient

evidence that the subgenera are not separated by fixed limits. From the peculiarities of certain species, such as *aurea* and *hypochaeridea* in *Catonia, patula, tingitana,* and *neglecta* in *Eucrepis,* and *albida* and *fontiana* in *Barkhausia,* it is clear that *Catonia* tends to merge into *Eucrepis* and the latter into *Barkhausia.* From such evidence it appears highly probable that the three 5-paired phylogenetic lines, one in each subgenus, had their origin in a common nexus. At any rate the genus must be looked upon as a natural unit.

9. *Chromosome morphology in Crepis.*—The chromosomes of *Crepis* species are of three distinct types, namely, those with a subterminal constriction, those with a subterminal constriction and bearing a satellite, and those with a median constriction. By comparing total length and relative length of the arms, chromosomes of the first general type are subdivided into classes known as A, B, and C. The satellite-bearing chromosome is called D and the small median-constricted chromosome, E. The only important exception to this general scheme is that in three subgroups under *Eucrepis* the large A chromosome has a median constriction.

10. *The basic genom.*—All the 5-paired species have one pair each of chromosome types A, B, C, D, E.

11. *Derived genoms and modes of derivation.*—All the 4-paired species have types A, B, C, D. The two 3-paired species have A, B or C, and D. The 6-paired species are variable. In *Catonia* they seem to have two pairs of A chromosomes, one or two pairs respectively of B or C types, and one pair of D's. In *Eucrepis* they have one, two, or three pairs of A type (sometimes with median constriction, sometimes with a satellite or compound), one, two, or no pairs of D type, and no, one, or two pairs of B, C, and E types. This evidence on composition of the 6-paired genoms indicates that these species were derived from 5-paired ancestors through hybridization, and that 12 is not a primitive number in *Crepis.* The 7-paired species have A, B, C, D, and E types with duplication of C, D, or E. This also suggests hybrid origin for these species and indicates that 14 is not a primitive number. All 8-paired species, so far as known, have only A, B, C, and D types and are polyploids. Analysis of distribution of chromosome types in the higher-numbered species has not been attempted, but dissimilarity of the satellite-bearing chromosomes in 11-paired American species adds sufficient proof of their origin through interspecific hybridization and amphidiploidy. Similar evidence is found in the two Old World octoploid species, *C. biennis* and *C. ciliata.*

12. *Chromosome morphology and phylogeny in Crepis.*—(*a*) Morphologically similar species have similar chromosomes. (*b*) Similarity in chromosome types and in details of size and shape is an index of phylogenetic relationship. (*c*) Both increase and decrease in chromosome size have occurred in the evolution of the genus. (*d*) There is a general ten-

dency toward reduction of size of chromosomes concurrently with reduction in size of the plant and reduction or specialization of organs. (*e*) There have been many changes in chromosome shape, as determined by relative length of the arms, and by these differences chromosomes of the same type from different species can be identified in hybrids. (*f*) This fact makes it possible, by analysis of the haploid genom, to determine the mode of origin of certain species.

13. *Chromosomes and taxonomy.*—Chromosome number and morphology is a taxonomic criterion of great value in this genus. But it must be used in connection with other available criteria such as comparative morphology and geographic distribution. Certainly, absolute identity of the chromosomes cannot be set up as of paramount importance in the classification of species, for specific entities are known in which the different forms exhibit differences in number, size, or shape of the chromosomes. The genus is still evolving and visible changes in the chromosomes are part of the process.

14. *Evolutionary processes in Crepis.*—(*a*) In view of the evidence here summarized that there is one most primitive chromosome number and type of genom in *Crepis,* it is clear that the primary evolutionary process which has operated in the history of the genus, as we now know it, is some mode of transformation by which 8– and 6–chromosome species have been derived from 10-chromosome ancestors. (*b*) Next in importance is interspecific hybridization and amphidiploidy. (*c*) Third comes polyploidy. (*d*) Superimposed upon and operating concurrently with the foregoing is gene mutation. (*e*) Origin of species with new chromosome numbers through transformation and through interspecific hybridization with amphidiploidy must have occurred early in the evolution of the genus. (*f*) All four processes have been at work during comparatively recent times.

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