

Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

Vol. 74

September, 1972

No. 799

INTRASPECIFIC VARIATION IN CHROMOSOMES OF SEDUM IN THE SOUTHWESTERN UNITED STATES

CHARLES H. UHL

Many species of *Sedum* include plants with different chromosome numbers (Uhl, 1961, 1970b). This intraspecific variation in number occurs in two patterns, here designated as established variation and casual variation. Established variation is represented by clear-cut geographical or ecological chromosome races, where any population clearly has a standard chromosome number, but populations in other areas or habitats may differ in the number of chromosomes in their sets (dysploidy) or in their number of chromosome sets (polyploidy). Casual variation is more random and accidental and is represented by individual plants that depart from the locally established chromosome race in ways that usually reflect some cytological instability or irregularity. The commonest examples are trisomy ($2n + 1$) and the presence of a variable number of small, extra, accessory, or "B" chromosomes.

Each established variant in chromosome number has a balanced, more or less stable and true-breeding outfit of chromosomes that has been tested and proved and that occupies a geographical or ecological portion of the range of the species. Most casual variants, on the other hand, have an unstable outfit of chromosomes that does not breed true to its own chromosomal type. Casual variants represent a sort of cytological "noise" or "static", and where

they are common they may sometimes blur or obscure the pattern of established variation. They may originate as segregants from hybrids with related species or between different established variants (chromosome races), or their occurrence may simply indicate that the population has not yet evolved to chromosomal stability. Doubtless each established variant first arose as a casual variant that was successful and eventually stabilized, and this process must still be going on. A relatively high background of casual variation might be expected in species with a significant amount of established variation. On the one hand, this reflects the continuation of the processes (instabilities) that originally led to the chromosome races (established variants), and on the other hand it may result from the occurrence of hybrids where the isolation was not yet complete.

The species of *Sedum* in the southwestern United States offer good examples of both types of chromosomal variation. This paper describes the chromosomes and the distribution of the chromosome races in five of these species: *S. cockerellii* Britton (including *S. griffithsii* Rose), *S. niveum* Davidson, *S. stelliforme* S. Wats., *S. wrightii* A. Gray, and *S. havardii* Rose. Probably all of these species, as well as other related species, occur in adjacent areas of northern Mexico, but material from there has been limited, except for *S. wrightii*. Living plants of these species are easy enough to identify, but many specimens of them are incorrectly identified in herbaria. In particular *S. cockerellii*, *S. stelliforme* and *S. wrightii* have been confused, and ranges given for these species in some Floras cannot be depended upon.

Most plants were collected in the field but grown in cultivation for a time before study. Counts were made from conventional aceto-carminic squash preparations of pollen mother cells. The photographs are from permanent preparations, all $\times 2000$. Voucher specimens are in the Wiegand Herbarium or Bailey Hortorium of Cornell University.

Clausen and Uhl (1943) classified *S. cockerellii* and *S. griffithsii*, as then known, into separate subsections, largely on the basis of a difference in chromosome number $n=16$ and $n=14$ or 29 , respectively). However, the two are very closely related, and in my opinion the additional chromosomal and morphological variation known today make it impractical to separate them. Therefore *S. cockerellii* is conceived broadly here, to include also *S. griffithsii* and the various other binomials earlier considered synonymous with one or the other of them (Clausen and Uhl, 1943).

Thus conceived, *S. cockerellii* has at least four chromosome races (established variants), with 14 , 16 , 29 or 30 gametic chromosomes. Probably the lone Texas population, with $n=15$, represents a fifth chromosome race. Each of these races occupies a definite geographic area, and in no case was more than one chromosome race found in the same range of mountains (Fig. 29). One or more extra chromosomes were found in plants from six widely separated localities. These casual variants occurred in populations in which the standard numbers (as confirmed by counts from other plants in four of the six populations) were $n=14$ (2 populations), $n=15$ (1 population), and $n=16$ (3 populations). In all but one case the extra chromosomes were smaller than the regular members of the set; they sometimes differed among themselves in size (e.g., Fig. 4) and occasionally paired with each other, although usually not with members of the standard set. Most of them seem to represent typical examples of accessory or "B" chromosomes. Their origin and function, if any, are completely unknown.

In general, plants of *S. cockerellii* from south central Arizona and northern Sonora have 14 pairs of chromosomes (Fig. 1). These include typical *S. griffithsii* (C5176). One plant from the Huachuca Mountains (U887A) had two small extra chromosomes that formed a bivalent in 7 of the 23 metaphase I plates examined (Fig. 2) but remained unpaired in the remaining 16 in the same anther (Fig. 3). Another plant from the same population (U887B) had the

standard 14 pairs. Still another plant, from Sycamore Canyon, southeast of Ruby (UC65.135), had three small, extra chromosomes (Fig. 4), but six other plants collected at various times from the same locality (U884, U1824) all had the standard 14 pairs.

The lone Texas population, which I believe is a new species record for the state, has $n=15$ (Fig. 5), although one of the four plants studied had a small, extra chromosome, possibly an accessory (Fig. 6). One pair of chromosomes is large, perhaps the result of combining most of two chromosomes from an ancestor with $n=16$.

Plants of *S. cockerellii* ranging from Oak Creek Canyon in north central Arizona to the White Mountains in the east central part of the state, mostly along or near the Mogollon Rim, as well as most collections from New Mexico, have $n=16$ (Fig. 7). These include plants from the vicinity of the type locality (U1315, U1316, C5254). Constrictions, apparently kinetochores, are detectable in some chromosomes of mitotic metaphases ($2n=32$, Fig. 8). Thus there is no reason to believe that diffuse or multiple kinetochores are related to the dysploidy in this species. A plant from the White Mountains of east central Arizona had a small accessory chromosome (U1155, Fig. 9), but plants from six other localities in the same mountains all had the standard 16 pairs. One plant from the Jemez Mountains of north central New Mexico had a small accessory chromosome (U1147G) and another from the same locality (C5281) had several (six in Fig. 10), but seven other plants from the same population had the standard 16 pairs (U1147A, B, C, D, E, F, H). Still another plant, from the Sangre de Cristo Range in northern New Mexico, had probably four extra chromosomes (U1133, Fig. 11). Since these were large enough to represent standard chromosomes, and since they appeared often to enter into multivalent formation with regular chromosomes (Fig. 12), the plant is possibly a quadruple trisomic ($2n+4$), perhaps descended from a triploid.

In the Mule Mountains (near Bisbee), in the Chiricahuas,

on Mount Graham, and on Kitt Peak in the Quinlan Mountains, all in southern Arizona, *S. cockerellii* has $n=29$ (Fig. 13). Plants from the Sierra Blanca Range in southern New Mexico have $n=30$ (Fig. 14). In these two tetraploid chromosome races univalents and multivalents are formed occasionally and make it difficult to detect any casual variation in chromosome number. None was noted in the 18 tetraploid collections studied.

S. niveum is closely related to *S. cockerellii* (Clausen and Uhl, 1943). High in the San Bernardino and Santa Rosa Mountains of southern California this endemic species has $n=16$ (Fig. 15), as does one race of *S. cockerellii*. *S. niveum* has recently been discovered about 200 miles to the south, high in the Sierra San Pedro Martir of northern Baja California (Moran, 1969). Here it is octoploid, with $n=64$ (Fig. 16), but occasionally forming a few multivalents and univalents at meiosis.

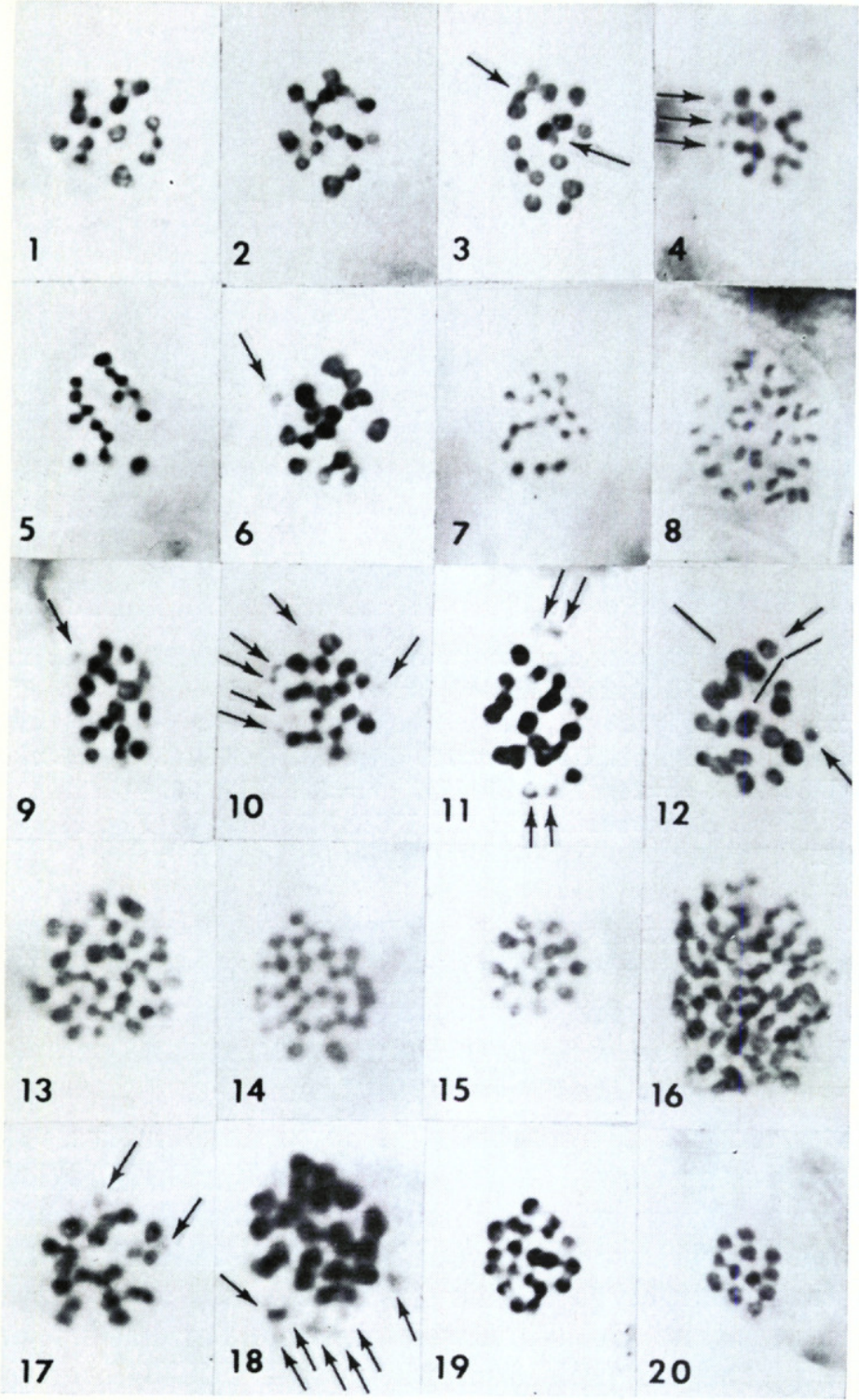
At one of its two type localities, Carr Peak in the Huachuca Mountains of southeastern Arizona, *S. stelliforme* has $n=20$, plus a variable number of accessory chromosomes, two to seven in different plants, (Figs. 17, 18). Another plant, probably this species, from more than 400 miles to the southeast in southern Chihuahua, Mexico, also had $n=20$ (Fig. 19), plus one or two extra, accessory chromosomes in some cells. Very similar plants from the White Mountains of east central Arizona and from the Black Range in southwestern New Mexico are considered for the present to be also the same species, but they all have $n=12$ (Fig. 20). The cause and significance of the two different, apparently unrelated, chromosome numbers (established variants) in the species is not at all clear; perhaps closer morphological study may support their taxonomic separation. One plant from the Black Range (U1625A) had 8 small accessory chromosomes (six are shown in Fig. 21), but two other plants from the same population and plants from seven other populations in the same mountains all had $n=12$.

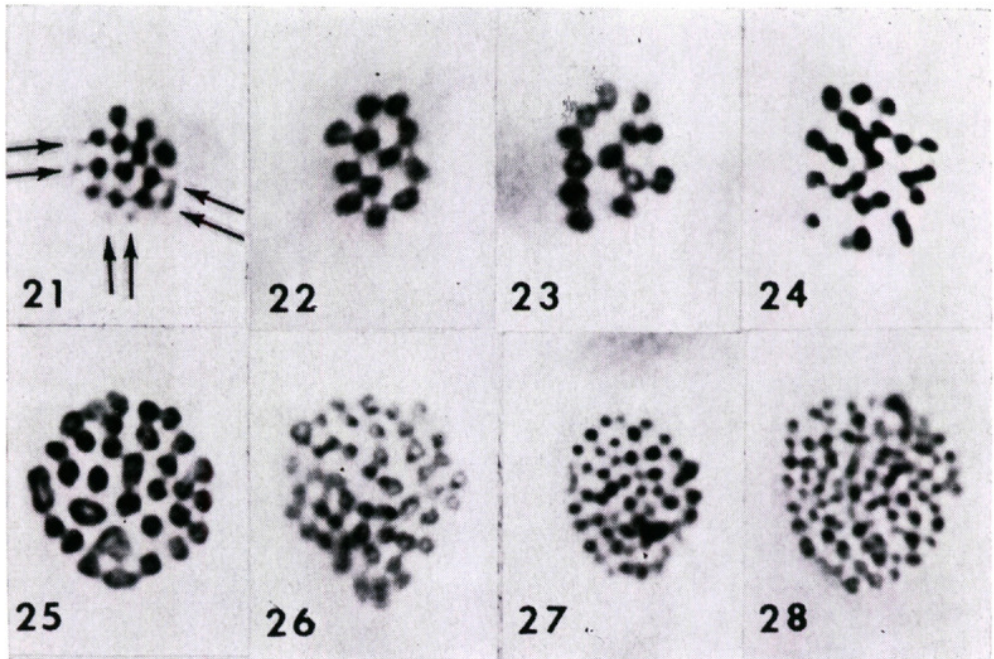
S. wrightii includes plants with four levels of ploidy

based on $x=12$, diploid through octoploid ($n=12, 24, 36$, and 48 ; Figs. 22, 24-26). No plants with accessory chromosomes or other casual variants were definitely noted, but one collection (UC52.1680) clearly had 13 pairs of chromosomes (Fig. 23), none of which was distinctively smaller than the others. Four plants collected later from what was presumed to be the same locality (U879) all had the standard diploid $n=12$. It is not certain whether the plant with $n=13$ is better considered another established variant or a casual variant. Univalents, multivalents, and close secondary associations are common enough to make exact counts difficult in some hexaploids ($n=36$) and octoploids ($n=48$). Probably these are autopolyploids. Autopolyploidy has been reported in *S. ternatum* (Baldwin, 1936; Uhl, 1970b), and, on the basis of evidence from chromosome pairing in hybrids, it appears to be common in the Mexican Crassulaceae (Uhl, 1970a, and unpub.).

The four principal chromosome types (established variants) of *S. wrightii* are not as discrete geographically (Fig. 30) as those of *S. cockerellii* and *S. stelliforme* (Fig. 29). Only diploids were found in southern New Mexico, and they occur also in the Davis Mountains of western Texas and in the vicinity of Saltillo, Coahuila, Mexico. Tetraploids ($n=24$) were found at the presumed type locality (U882, near El Paso), near Marathon, Texas, in the

Figs. 1-20. *Sedum* chromosomes in pollen mother cells at metaphase I (except Figs. 8, 16), $\times 2000$. Arrows identify univalents and/or accessory ("B") chromosomes. Figs. 1-14. *S. cockerellii*. Fig. 1. U883, $n=14$. Fig. 2. U887A, $n=15$. Fig. 3. U887A, $n=14+2_1$. Fig. 4. UC65.135, $n=14+3B$. Fig. 5. U880C, $n=15$. Fig. 6. U880B, $n=15+1B$. Fig. 7. U900, $n=16$. Fig. 8. U900, mitosis in anther wall, $2n=32$. Note constrictions (kinetochores) in some chromosomes. Fig. 9. U1155, $n=16+1B$. Fig. 10. C5281, $n=16+6B$. Fig. 11. U1133, $n=16+4B$. Fig. 12. U1133, 2_{III} (identified by lines) $+14_{II}+2_1$. Fig. 13. U888, $n=29$. Fig. 14. U1307, $n=30$. Figs. 15-16. *S. niveum*. Fig. 15. M345, $n=16$. Fig. 16. M15333, $n=64$ (Metaphase II). Figs. 17-20. *S. stelliforme*. Fig. 17. U1680A, $n=20+2B$. Fig. 18. U1680C, $n=20+7B$. Fig. 19. U2051, $n=20$. Fig. 20. U1312, $n=12$.





Figs. 21-28. *Sedum* chromosomes in pollen mother cells at metaphase I, $\times 2000$. Arrows identify univalents and/or accessory ("B") chromosomes. Fig. 21. *S. stelliforme*. U1625A, $n=12+6B$. Fig. 22-26. *S. wrightii*. Fig. 22. U879, $n=12$. Fig. 23. UC52.1680, $n=13$. Fig. 24. UC53.407, $n=24$. Fig. 25. U877, $n=36$. Fig. 26. M6317, $n=48$. Figs. 27-28. *S. havardii*. Fig. 27. UC52.1679, $n=54$. Fig. 28. U876, $n=81$.

Sierra del Carmen (across the Rio Grande from Big Bend) and in the Sierra Madre Oriental in southern Nuevo Leon, Mexico. Hexaploids ($n=36$) were found at Big Bend and 135 miles to the east, near Del Rio, Texas, and octoploids ($n=48$) only in southern Nuevo Leon.

S. havardii is apparently of Mexican affinities. It is known in the United States only in the Big Bend region of western Texas, where plants with 54 and 81 gametic chromosomes have been found (Figs. 27, 28). Presumably the basic karyotype of this species consists of 27 chromosomes, but no collection with this number has yet been found. The only collection with $n=81$ (U876) was made only 1 1/2 miles from another (U875) with $n=54$. Thus it is not yet clear whether the plants with the different numbers really represent established chromosomal vari-

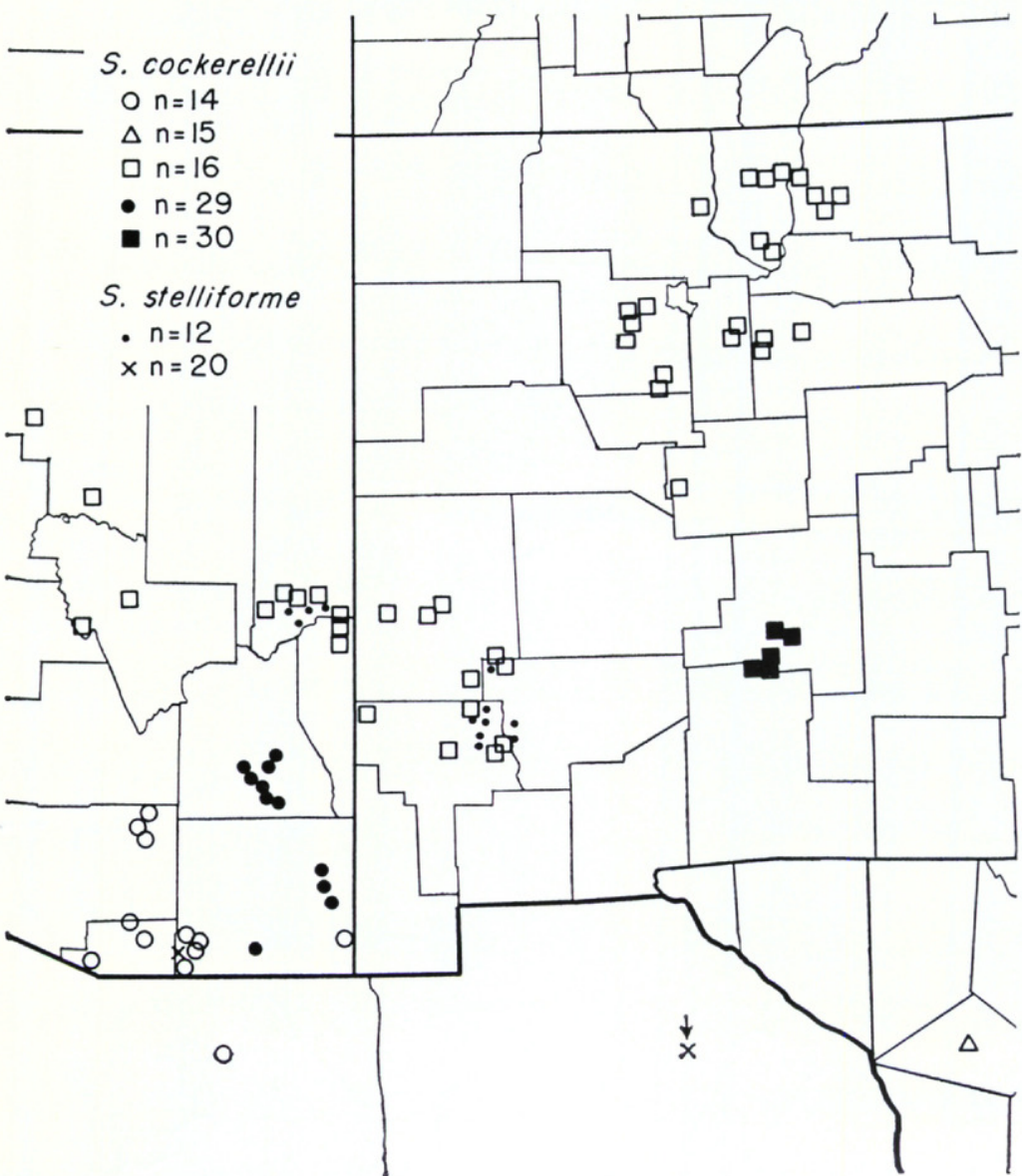


Fig. 29. Distribution of chromosome races (established variants) of *Sedum cockerellii* (s. lat.) and *S. stelliforme* in New Mexico, Arizona and adjacent regions.

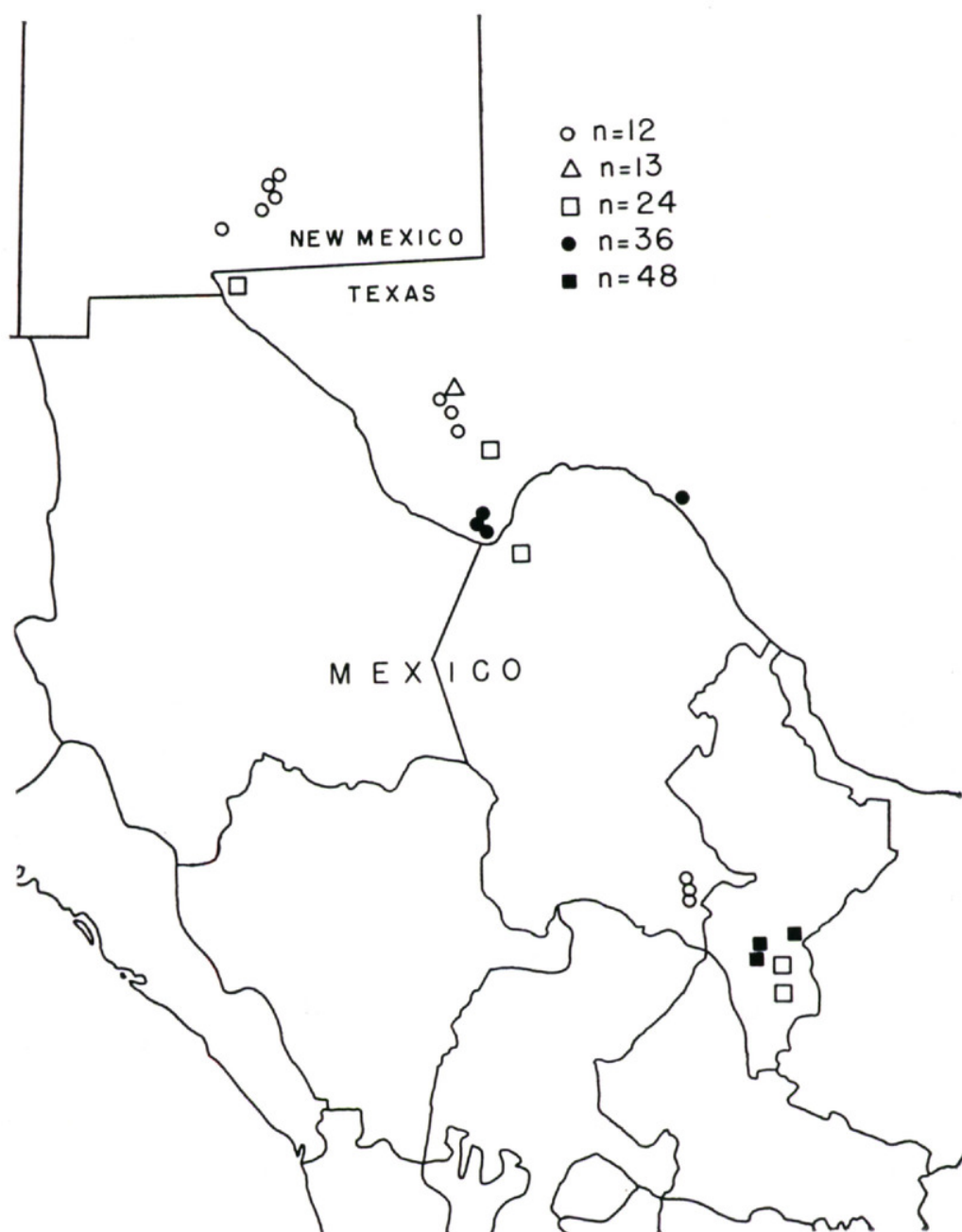


Fig. 30. Distribution of chromosome races of *Sedum wrightii* in New Mexico, Texas and northeastern Mexico.

ants (races) or only two samples from a large population containing casual variants in ploidy. Two of the most similar species are *S. diffusum* ($x=19$) of northeastern Mexico and *S. alamosanum* ($x=18$) of northwestern Mexico, both of which also have polyploid races.

Plants of *S. cockerellii* with $n=16$ (U1690) have been found within inches of *S. stelliforme* with $n=12$ (U1691) in the White Mountains, and plants of *S. griffithsii* (here included in *S. cockerellii*) with $n=14$ on Carr Peak in the Huachuca Mountains (U1679) are no more than a mile from plants of *S. stelliforme* that have $n=20$ + accessories (U1680). At two localities on opposite sides of Red River Pass in the Sangre de Cristo Range of northern New Mexico, *S. cockerellii* with $n=16$ (U1134, U1138) was found within inches of the yellow-flowered, tetraploid *S. lanceolatum*, also $n=16$ (U1135, U1139), with both species in flower together. This locality is near the northern limit of the range of *S. cockerellii*, near the southern limit for *S. lanceolatum*.

S. cockerellii was never found close to *S. wrightii*, although perhaps the two might occur together in the Davis or Organ Mountains. *S. cockerellii* generally occurs in the Transition and Canadian Zones, nearly always near streams that flow all year, whereas *S. wrightii* is generally a plant of the warmer and drier Sonoran Zone (Clausen and Uhl, 1943). However, in the Sacramento Mountains about Cloudcroft, New Mexico, diploid *S. wrightii* ($n=12$) occurs at higher elevations (four collections: 8000-8400') than does *S. cockerellii* 20-30 miles north in the Sierra Blanca Range about Ruidoso (five collections: 7100-7600'). Each species was found in only the one range in this area and not found in the other. *S. wrightii* (hexaploid, U873) occurs with *S. havardii* (U875) in the Chisos Mountains of Big Bend National Park and with other species in Mexico.

Each of the five species has two or more chromosome races (established variants). Polyploidy definitely occurs in four of the five, and it may also account in some degree

for the difference between the races of *S. stelliforme* with $n=12$ and $n=20 + B$'s. Extra chromosomes, usually accessories, were found in some diploid plants in three species. Probably this sort of casual variation should be expected where so much established variation also occurs. In the same region *Graptopetalum rusbyi* of Arizona also includes polyploids and variations from strict diploidy (Uhl, 1970a).

Apparently quite a few structural changes have occurred in the chromosomes of these species. Structural rearrangements must have been involved in the evolution of the different numbers (14, 15, 16) in diploid *S. cockerellii*. Chromosome bridges at anaphase, which usually indicate heterozygosity for an inversion, were not especially looked for, but they were common in two plants of this species (U887A and C5176).

Differences in chromosome number interfere with free interchange of genetic material and thus they represent a means of reproductive isolation that may eventually lead to new taxonomic species. However, anointing each established variant (chromosome race) as a different taxonomic species, as some (e.g., Löve, 1951) have favored for other groups, seems undesirable here. It would increase the number of species reported on from five to at least 15, and many of the splinter species probably could not be distinguished without cytological study. Thus it seems better to take a broad concept of these species. The chromosomal variants are considered to indicate that evolutionary changes are actively occurring in the five species, but the changes are considered not yet to have crossed the threshold of the practical, taxonomic species. More careful morphological study, such as that now being carried out by my colleague, Professor R. T. Clausen, may some day require modification of this conclusion for one or more of the five species.

The large proportion of chromosomal variants in these species finds a parallel in certain other species of *Sedum* in the United States, e.g., *S. glaucophyllum* and *S. terna-*

tum (Uhl, 1970b), and also *S. lanceolatum* (Uhl, unpub.). However, it contrasts sharply with the situation in still others. For example, in 78 collections of *S. spathulifolium*, ranging from Vancouver Island to southern California and exhibiting considerable variation in such characters as leaf thickness, width, crowding and glaucosity, no established variants were found, and all plants but two had seemingly identical karyotypes with $n=15$ (Uhl, unpub.). The only two exceptions were both casual variants: a plant with $n=14$ in a population that also included a standard plant, and a triploid. Seventy-nine other collections, representing five other species related to *S. spathulifolium*, also all had $n=15$, with no variants, either established or casual. However, one related species had $n=30$ and another $n=45$. It is not clear whether the relative scarcity of non-standard chromosome complements in these species means that they are produced less frequently or that they survive less well, or both. At any rate, the karyotype here has remained stable in number and probably also in form during the evolution of enough morphological diversity that six species are recognized and while spreading 1100 miles apart. This stability must reflect differences in the nature of the genetic and chromosomal changes that have contributed to evolution in *S. spathulifolium* and its relatives (subgenus *Gormania*), contrasted with those prevailing in most of the species described earlier.

Summary

Variation in chromosome number is found within each of five species of *Sedum* of the southwestern United States. Established variation is represented by polyploid and/or dysploid geographic chromosome races, two to five for each species. Casual variation, represented by the occurrence of occasional plants that are trisomic or that bear accessory chromosomes, was found in two, possibly three, species. Successful casual variants can become established variants (races). Although differences in chromosome number are accompanied by some degree of reproductive isolation, rec-

ognition of each chromosomal variant as a different species does not seem appropriate in these actively evolving cases.

Acknowledgement

I thank those who have provided some of the plants reported on here, especially Dr. Reid Moran, of the Natural History Museum, San Diego (M nos.), and Mr. Paul Hutchison, formerly of the University of California Botanical Garden, Berkeley (UC nos.). Publication was assisted by the L. W. Sharp Fund of Cornell University.

COLLECTIONS STUDIED

S. cockerellii Britton

Arizona:

- U894 $n=14$ Pima Co. 4 mi. N. of road summit, Mt. Lemmon, Santa Catalina Mts., 6240'.
 U893 $n=14$ Pima Co. 0.8 mi. below Mt. Lemmon Lodge, 7520'.
 UC52.1674 $n=14$ Same locality, (E. R. Blakely).
 U892 $n=14$ Pima Co., Bear Canyon, 15 mi. by road S. of Mt. Lemmon Lodge, 5480'.
 U883 $n=14$ Santa Cruz Co., Madera Canyon, Santa Rita Mts., 6400'.
 C5176 $n=14$ Santa Cruz Co., near summit, Baldy Peak, Santa Rita Mts., 8900'. ? Topotype of *S. griffithsii* Rose, (R. T. Clausen).
 U884 $n=14$ (5 plants) Santa Cruz Co., Sycamore Canyon, 5 mi. S.E. of Ruby, Atasco Mts., 3960'.
 U1824 $n=14$ Same locality, (A. M. Phillips III).
 UC65.135 $n=14+3B$ Same locality, (D. M. Hutt).
 U885 $n=14$ (2 plants) Santa Cruz Co., Sonoita Cr., 3 mi. S.W. of Patagonia, 3920'.
 U886 $n=14$ Santa Cruz Co., Mile 16 N.E. of Nogales, 2.8 mi S.W. of Patagonia, 3900'.
 U887A $n=14+2$, Cochise Co., Ramsay Canyon, Huachuca Mts., 6000'.
 U887B $n=14$ Same locality.
 U1681 $n=14$ Cochise Co., Reef Mine, Upper Carr Canyon, Huachuca Mts., 7100'.
 U1679 $n=14$ Cochise Co., N. slope of Carr Peak, Huachuca Mts., 7700'.
 C5189 $n=14$ Cochise Co. Same locality, (R. T. Clausen).

- UC52.1678 $n=14$ Cochise Co., Guadalupe Canyon, Guadalupe Mts., 4300', (E. R. Blakely).

Mexico:

- M14849 $n=14$ Sonora. Cerro Colorado, S.E. of Cananea, (C. Glass and D. Gold).

Arizona:

- U900 $n=16$ Coconino Co., Oak Creek Canyon, 12 mi. N. of Sedona, 5600'.
U1617 $n=16$ Coconino Co., Macks Crossing, E. Clear Cr., 15 mi. N.E. of Clints Well, 6260'.
UC52.1673 $n=16$ Gila Co., N. peak of Four peaks Mt., Mazatzal Mts., 7645', (E. R. Blakely).
U1688 $n=16$ Gila Co., Workman Creek Falls, 44 mi. N. of Miami, Sierra Ancha, 6600'.
U1618 $n=16$ Apache Co., near dam, Hawley Lake, White Mts., 8200'.
U1694 $n=16$ Apache Co., Snake Cr., 19 mi. E. of McNary, White Mts.
U1158 $n=16$ Apache Co., 3.8 mi. N. of Greer, White Mts., 8400'.
U1690 $n=16$ Apache Co., 14 mi. W. of Alpine, White Mts., 8500'.
U1157 $n=16$ Greenlee Co., 6.6 mi. S. of Alpine, 7950'.
U1156 $n=16$ Greenlee Co., 10.3 mi. S. of Alpine, 7700'.
U1155 $n=16+1B$ Greenlee Co., 2.7 mi. N. of Hannagan Meadows, White Mts., 8800'.

New Mexico:

- U1152 $n=16$ Catron Co., 10 1/2 mi. W. of Reserve, San Francisco Mts., 7200'.
U1151 $n=16$ Catron Co., Tularosa R., 1 mi. E. of Aragon, 6750'.
U1150 $n=16$ Catron Co., Tularosa R., 3 mi. E. of Aragon, 6900'.
U1621 $n=16$ Catron Co., Wall L., 9 mi. S. of Beaverhead, Black Range, 6400'.
U1619 $n=16$ Sierra Co., Poverty Can., 19 mi. N.W. of Winston, Black Range, 7500'.
U1153 $n=16$ Grant Co., 4 mi. W. of Mule Cr., San Francisco Mts., 5800'.
U1622 $n=16$ Grant Co., Black Canyon Forest Camp, 32 mi. N. of Mimbres, Black Range, 6770'.
U1309 $n=16$ Grant Co., 2.5 mi. N. of Pinos Altos, Pinos Altos Range, 6600'.
U1310 $n=16$ Grant Co., Iron Cr., 6.6 mi. W. of Emory Pass, Black Range, 6800'.
U1311 $n=16$ Grant Co., Iron Cr., 5.1 mi. W. of Emory Pass, 7200'.
U1314 $n=16$ Torrance Co., Red Canyon Forest Camp, 7 mi. W. of Manzano, Manzano Mts., 7800'.

- U1148 $n=16$ Sandoval Co., Jemez R. at Soda Spring, 1.6 mi. N. of Jemez Springs, 6350'.
- C5281 $n=16+3-6B$ Sandoval Co., 4 mi. N. of Battleship Rock, near LaCueva, Jemez Mts., 7700', (R. T. Clausen).
- U1147 $n=16$ (7 plants) $n=16+1B$ (1 plant) Sandoval Co., LaCueva, (Probably same locality as preceding).
- U1146 $n=16$ Sandoval Co., Jemez Falls, 7850'.
- U1145 $n=16$ Sandoval Co., Las Conchas Forest Camp, Jemez Mts., 8400'.
- U1149 $n=16$ Sandoval Co., Las Huertas Cr., 6 mi. S. of Placitas, Sandia Mts., 7830'.
- C4633b $n=16$ (2 plants) Sandoval Co., Ellis Brook, N. side Sandia Mts., (R. T. Clausen).
- C4633a $n=16$ Sandoval Co., Sandia Crest, Sandia Mts., 10,400', (R. T. Clausen).
- U1315 $n=16$ Santa Fe Co., 6 mi. N.E. of Santa Fe, 7500'.
- U1316 $n=16$ Santa Fe Co., 9 mi. N.E. of Santa Fe, Black Canyon Forest Camp, 8300'.
- U1143 $n=16$ San Miguel Co., E. side Pecos R. at bridge 6.4 mi. N. of Pecos, 7200'.
- C5254 $n=16$ San Miguel Co., Pecos R., 5 mi. S. of Terrero, 7500', (R. T. Clausen).
- U1142 $n=16$ San Miguel Co., Gallinas Cr., 1/2 mi. W. of Montezuma, 6750'.
- U1317 $n=16$ Rio Arriba Co., Rio Vallecitos, 5.5 mi. N. of LaMadera, Ortega Mts., 6900'.
- U1138 $n=16$ Taos Co., S. side Red River, 2.7 mi. E. of Questa, 7550'.
- U1137 $n=16$ Taos Co., S. side of Red River, 4.5 mi. W. of Red River village, 8150'.
- U1136 $n=16$ Taos Co., Mouth of Mallette Canyon, village of Red River, 8650'.
- U1140 $n=16$ Taos Co., S. side Rio Pueblo at Comales Forest Camp, 7850'.
- U1141 $n=16$ Taos Co., N. side Rio Pueblo, 2.2 mi. N.W. of Tres Ritos, 8250'.
- U1134 $n=16$ Colfax Co., 2.6 mi. E. of Red River Pass, Sangre de Cristo Range, 8900'.
- U1133 $n=16+4$ Colfax Co., Cimarron Cr., 5 mi. E. of Eagle Nest, 7850'.
- U1132 $n=16$ Colfax Co., Cimarron Canyon, 5 mi. W. of Ute Park, 7750'.
- U1131 $n=16$ Colfax Co., Cimarron Cr., 1 mi. W. of Ute Park, 7550'.

Texas:

- U880 $n=15$ (2 plants) $n=15+1$ (1 plant) Jeff Davis Co., Madera Canyon, 25 mi. W.NW. of Fort Davis, Davis Mts., 5800'. 1961.
 U1633 $n=15$ Same locality, 1967.

Arizona:

- U1685 $n=29$ 1.6 mi. SE of Columbine Ranger Sta., Mt. Graham, 9215'.
 U1684 $n=29$ Graham Co., Grant Creek, Swift Trail, Mt. Graham, 8750'.
 U1683 $n=29$ Graham Co., Near Snow Flat, Swift Trail, Mt. Graham, 9000'.
 U1686 $n=29$ Graham Co., 1.7 mi. N.W. of Ladybug Saddle, Swift Trail Mt. Graham, 8800'.
 U1682 $n=29$ Graham Co., 1 mi. below Turkey Flat, Swift Trail, Mt. Graham, 7300'.
 U1926 $n=29$ Graham Co., Marijilda Canyon, Mt. Graham, 8200', (A. M. Phillips III).
 U1927 $n=29$ Graham Co., Marijilda Canyon, Mt. Graham, 4800', (A. M. Phillips III).
 C5224 $n=29$ Cochise Co., S. of Rustler Park, Chiricahua Mts., 8500', (R. T. Clausen).
 UC65.144 $n=29$ Cochise Co., 1/2 mi. below Onion Saddle, Chiricahua Mts., 7300', (D. Hutt 1260).
 U1678 $n=29$ Cochise Co., S. Fork, Cave Cr., 3 mi. S.W. of Portal, Chiricahua Mts., 5150'.
 U1253 $n=29$ Cochise Co., Chiricahua Mts., (C. English).
 U888 $n=29$ (2 plants) Cochise Co., 1/2 mi. N. of Mule Pass, Mule Mts., N. of Bisbee, 5840'.

New Mexico:

- U1629 $n=30$ Lincoln Co., Bonito Cr., 7.2 mi. W. of Angus, Sierra Blanca, 7500'.
 U1628 $n=30$ Lincoln Co., 3.1 mi. W. of Angus, 7100'.
 U1307 $n=30$ Lincoln Co., Eagle Cr., 2.5 mi. W. of Alto, Sierra Blanca, 7600'.
 U1304 $n=30$ Same, 1.5 mi. W. of Alto, 7450'.
 U1630 $n=30$ Otero Co., Carrizo Cr., Mescalero Apache Indian Res., 2.2 mi. W. of Ruidoso, Sierra Blanca, 7200'.

*S. niveum Davidson***California:**

- C4759 $n=16$ San Bernardino Co., Sugar Loaf Peak, S. Bernardino Mts., 7000', (R. T. Clausen).
 C4759b $n=16$ Same, Dollar Lake, 9300', (R. T. Clausen).

- U919 $n=16$ San Bernardino Co., above Jenks Lake, 8000', (D. Verity).
 M345 $n=16$ Riverside Co., Santa Rosa Peak, Santa Rosa Mts., (P. A. Munz).
 M15346 $n=16$ Riverside Co., 1 mi. N.W. of Toro Peak, Santa Rosa Mts., 7450', (R. Moran).

Mexico:

- M15333 $n=64$ Baja California, Observatory Peak, Sierra San Pedro Martir, 9300', (R. Moran).
 M15682 $n=64$ prob. Same, N. slope, 8400'. (R. Moran).

S. stelliforme S. Wats.

Arizona:

- U1680 $n=20+2-7B$ (5 plants) Cochise Co., N.E. slope Carr Peak, Huachuca Mts., 8300'. **TOPOTYPE**
 C5192 $n=20+2B$ Same Locality, (R. T. Clausen).
 U1693 $n=12$ Apache Co., N. side Crescent L., White Mts., 9100'.
 U1689 $n=12$ Apache Co., Cienega Redondo, 16 mi. W. of Alpine, White Mts., 8950'.
 U1691 $n=12$ Apache Co., 1 1/2 mi. W. of Three Forks, Black R., 14 mi. W. of Alpine, 8550'.
 U1692 $n=12$ Apache Co., Williams Valley, 7.2 mi. W. of Alpine, 8650'.

Mexico:

- U2051 $n=20+1$ or 2B Chihuahua, 55 mi. W. of San Francisco del Oro, (M. Kimnach and F. K. Brandt 1058).

New Mexico:

- U1623 $n=12$ Grant Co., 1.4 mi. S. of Black Canyon Forest Camp, Black Range, 7000'.
 U1624 $n=12$ Grant Co., 2.6 mi. S. of same, 7300'.
 U1625 $n=12$ (2 plants) Grant Co., 3.3 mi. N. of Rocky Canyon Forest Camp, Black Range, 7800'.
 U1625A $n=12+8B$ Same locality.
 U1626 $n=12$ Grant Co., 1.2 mi. N. of same, 7600'.
 U1627 $n=12$ Grant Co., 2.9 mi. S. of same, 7400'.
 U1312 $n=12$ Grant Co., 2.8 mi. W. of Emory Pass, Black Range, 7600'.
 U1313 $n=12$ Sierra Co., 1 mi. N. of Emory Pass, Black Range, 9000'.
 U1620 $n=12$ Sierra Co., N. side of Boiler Peak, 3.2 mi. W. of Continental Divide, Black Range, 7900'.

S. wrightii A. Gray

New Mexico:

- U1631 $n=12$ Otero Co., Silver Springs Canyon, 7.8 mi. N.E. of Cloudcroft, Sacramento Mts., 8000'.

- U1303 $n=12$ Otero Co., Silver Springs Canyon, 5 mi. N.E. of Cloudcroft, 8400'.
 U1302 $n=12$ Otero Co., Cox Canyon, 5.2 mi. S.E. of Cloudcroft, 8150'.
 U1632 $n=12$ Otero Co., Upper Peñasco Canyon, 13 1/2 mi. S. of Cloudcroft, 8400'.
 C5241 $n=12$ Dona Ana Co., Canyon at La Cueva, Organ Mts., (R. T. Clausen).

Texas:

- U882 $n=24$ El Paso Co., McKelligon Canyon, N. of El Paso, S. side of Franklin Mts., 5400', TOPOTYPE.
 C364 $n=12$ Jeff Davis Co., Fern Canyon, Davis Mts.
 UC52.1680 $n=13$ Jeff Davis Co., 20 mi. N. of Alpine, Davis Mts., 4900', (E. R. Blakely 1378).
 U879 $n=12$ (4 plants) Jeff Davis Co., 5 mi. S. of Fort Davis, Davis Mts., 4800', (Same locality as preceding?).
 U878 $n=12$ Brewster Co., Sunny Glen, 6 mi. W.NW. of Alpine, 4800'.
 U1676 $n=24$ Brewster Co., 3.4 mi. S. of US 90 at Marathon, 4100'.
 U877, U1675 $n=36$ Brewster Co., Green Gulch, N. of Panther Gap, Chisos Mts., Big Bend National Park, 5600'.
 U873 $n=36$ Upper Boot Canyon, Chisos Mts., 6900'.
 UC52.1672 $n=36$ E. side of Emory Peak, Chisos Mts., 7000', (E. R. Blakely 1402).
 C5298 $n=36$ Chinese Wall, Chisos Mts., (R. T. Clausen).
 U868 $n=36$ Val Verde Co., E. side of Devils River, 8 mi. N.W. of Del Rio, 1100'.
 UC54.1334 $n=36$ Same locality, (J. B. Perry).

Mexico:

- UC53.407 $n=24$ Coahuila, 8 mi. S.W. of Piedra Blanca, Sierra del Carmen, 7000', (Ward Russell).
 U1497 $n=12$ Coahuila, Chorro Canyon, 27 km. S.E. of Saltillo, ca. 6500'.
 U1501 $n=12$ Coahuila, Chorro Canyon, 33 km. S.E. of Saltillo, ca. 7000'.
 M7825 $n=12$ Coahuila, Chorro Canyon, (R. Moran).
 M6317 $n=48$ Nuevo Leon, San Jose de Raices, (R. Moran).
 U1494 $n=45-48$ Nuevo Leon, 6 km. S. of San Jose de Raices, 6100'.
 U1916 $n=48$ Nuevo Leon, 3 km. W. of Iturbide, 5400'.
 U1914 $n=24$ Nuevo Leon, 16 mi. N. of Ascension, 7900'.
 U1912 $n=24$ Nuevo Leon, 30 mi. N. of Doctor Arroyo, 4 mi. N. of La Escondida, 5900'.

Sedum havardii Rose

Texas:

- U875 $n=54$ Brewster Co., Chisos Mts., Big Bend National Park:
N. of Boot Spring, 6900'.
U876 $n=81$ 1 1/4 mi. S. of Boot Spring, 7000'.
UC52.1679 $n=54$ E. side of Emory Peak, 7000', (E. R. Blakely).
U1674 $n=54$ Above E. side of Panther Pass, N. side of Casa
Grande, 6200'.
C363 $n=54$ Green Gulch, 5500'.

LITERATURE CITED

- BALDWIN, J. T., JR. 1936. Polyploidy in *Sedum ternatum*. J. Hered. 27: 241-248.
CLAUSEN, R. T., and C. H. UHL. 1943. Revision of *Sedum cocker-elli* and related species. Brittonia 5: 33-46.
LÖVE, A. 1951. Taxonomical evaluation of polyploids. Caryologia 3: 263-284.
MORAN, R. 1969. *Sedum* in Baja California. J. Cactus & Succulent Soc. Am. 41: 20-25.
UHL, C. H. 1961. Some cytotaxonomic problems in the Crassulaceae. Evolution 15: 375-377.
———. 1970a. Chromosomes of *Graptopetalum* and *Thompsonella* (Crassulaceae). Am. J. Bot. 57: 1115-1121.
———. 1970b. Heteroploidy in *Sedum glaucophyllum*. Rhodora 72: 460-479.

DIVISION OF BIOLOGY

CORNELL UNIVERSITY

ITHACA, NEW YORK 14850



Uhl, Charles Harrison. 1972. "INTRASPECIFIC VARIATION IN CHROMOSOMES OF SEDUM IN THE SOUTHWESTERN USA." *Rhodora* 74, 301–320.

View This Item Online: <https://www.biodiversitylibrary.org/item/14694>

Permalink: <https://www.biodiversitylibrary.org/partpdf/123710>

Holding Institution

Missouri Botanical Garden, Peter H. Raven Library

Sponsored by

Missouri Botanical Garden

Copyright & Reuse

Copyright Status: In copyright. Digitized with the permission of the rights holder.

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.