

HETEROPLOIDY IN *SEDUM GLAUCOPHYLLUM*

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In the Crassulaceae differences in chromosome number are common, not only within genera but also often within species (Uhl, 1961). In many cases these differences take the form of a polyploid series among related species or within what, by the usual taxonomic criteria, appears to be the same species. Many cases of dysploidy also are known. In some cases because of extensive dysploidy even the basic or ancestral chromosome number cannot be determined with any confidence.

The species of *Sedum* native to the eastern United States offer several examples of heteroploidy, including both polyploidy and dysploidy. Baldwin has reported on the cytogeography of polyploidy in *S. ternatum* (1942b) and in *S. pulchellum* (1943). Uhl (1952) reported dysploidy in *S. rosea* (*sensu lato*), which includes a circumboreal race with $n=11$ and a North American race with $n=18$, both of them occurring in New York state. This paper reports the presence of heteroploidy, including both polyploidy and dysploidy, in *S. glaucophyllum*, with brief discussions of distribution and possible origin and of the chromosomes of some related species.

R. T. Clausen (1946) described *S. glaucophyllum* for plants of western Virginia and adjacent areas. The type locality is Mountain Lake, Giles Co., Virginia. Previously these plants had usually been identified as *S. nevii* Gray, a species which was originally based on plants from Alabama. *Sedum beyrichianum* Masters represents an earlier recognition of two taxa here, but only described *S. nevii* again (Clausen, 1946).

Sedum glaucophyllum is generally coarser than *S. nevii* (*sensu stricto*), with slightly broader, more glaucous leaves in denser rosettes. Separation of the two as species was supported by earlier reports of a difference in chromosome number, $n=6$ in plants from Alabama and $n=14$ in plants

from Virginia, including some from Mountain Lake (Baldwin, 1942a). Clausen (1946, 1949) has given detailed descriptions and a taxonomic history of the two species.

MATERIALS AND METHODS

Plants were collected sporadically between 1946 and 1968 and grown at Ithaca, New York. Their localities are mapped in Fig. 17 and listed in Table 1, arranged by counties, roughly from north to south and then from east to west. Conventional aceto-carminc squash preparations were made of meiosis in the pollen mother cells; the slides were studied and then made permanent. In most cases only one plant of a population was studied cytologically. In 13 of the 15 cases where two or more plants from the same population were studied the same number of chromosomes was found. One exception to this rule was an obvious case of chromosome doubling; the other involved apparent hybrids between the two principal chromosome races. The photographs (Figs. 1-16) are from permanent preparations, $\times 2000$. Voucher specimens of most collections are in the Wiegand Herbarium of Cornell University.

CYTOLOGY

Sedum glaucophyllum contains three chromosome races, with gametic numbers of 14, 22, and 28 (Figs. 1-4). Throughout the range, in all chromosome races, several large, mostly metacentric bivalents are conspicuous. The 14-chromosome race has one long metacentric bivalent and two that are slightly shorter (Figs. 1, 2). The 22-chromosome race has two long metacentric bivalents and three others that appear as considerably shorter rods, only about half as long (Figs. 3, 5, 6). In both races the remaining, smaller bivalents differ among themselves somewhat in size, but none are sufficiently distinctive to be consistently identified at meiosis. Thus the karyotypes of these two races differ not merely in number alone, but also in the structure of some of the longer chromosomes.

The large bivalents of *S. glaucophyllum* are very unusual

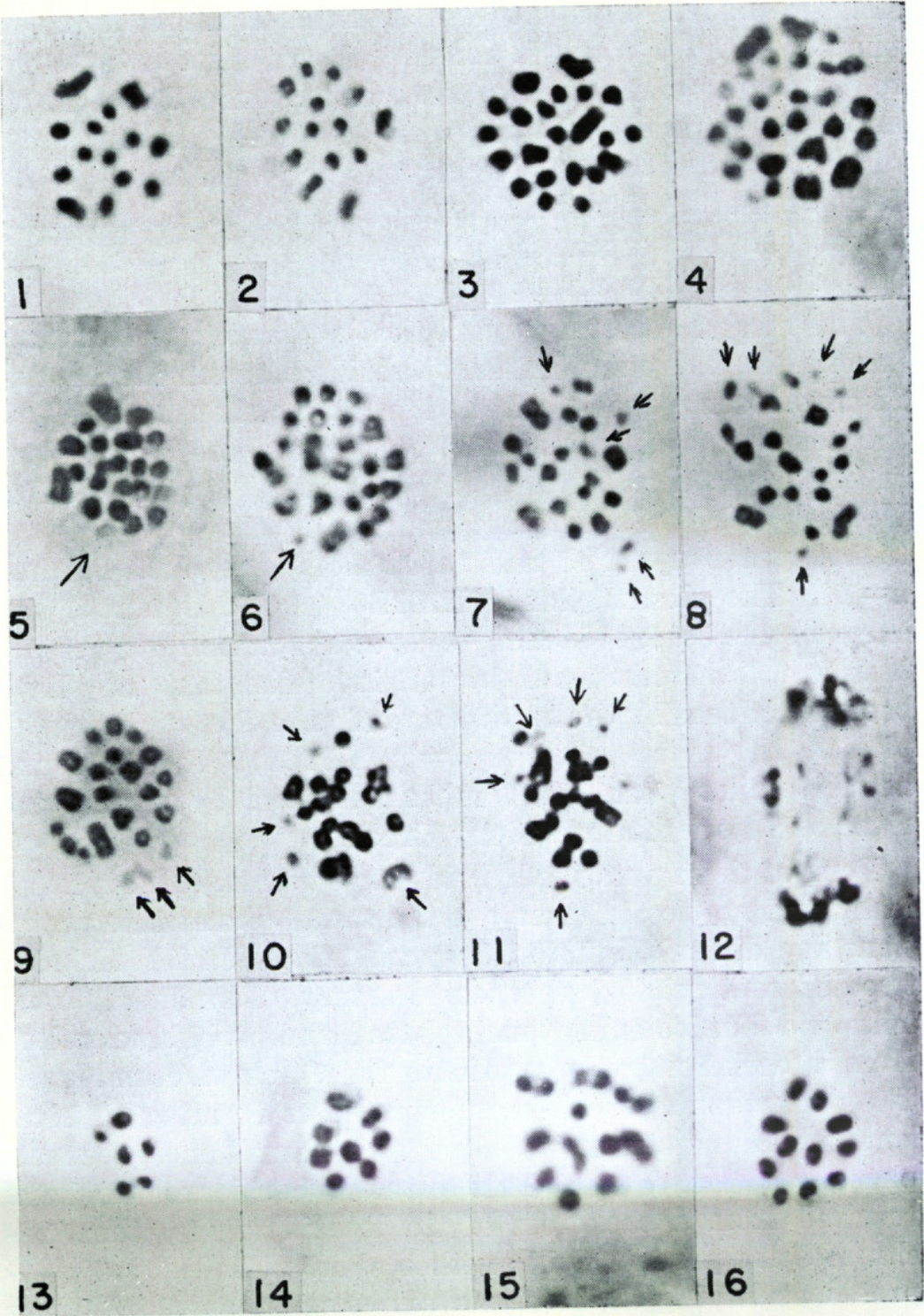
among the Crassulaceae, where as a general rule all bivalents look essentially round at meiotic metaphases and where usually no bivalents can be consistently identified. Baldwin (1942a), who found only the 14-chromosome race, figured the large chromosomes in root tip cells, but his interpretation apparently differs somewhat as to their number and form from that presented here, which is based strictly on meiotic material.

The race with $n=28$ bears six pairs of larger chromosomes, instead of three. Clearly these plants must have originated by chromosome doubling in an ancestor with $n=14$. This race was found only in a small area a few miles east of Clifton Forge, Virginia, along the lower Cowpasture River and on North Mountain to the east. Univalents and occasional multivalents are present in some metaphase I figures, and lagging chromosomes at anaphases I and II. The number of dyads on the metaphase II plates also seems to vary occasionally, as might be expected. This race has all of the cytological earmarks of an autotetraploid.

Only a few miles to the west, 8 miles north-northeast of Covington, a population was found (U268) that included plants with $n=22$ and $n=44$, another obvious case of chromosome doubling. The same sort of meiotic irregularities were seen in the plants with $n=44$ as in the ones with $n=28$.

Several other plants represent more or less accidental variants from the standard. One collection (U575) con-

Figs. 1-16. Chromosomes in pollen mother cells at metaphase I (except Fig. 12), $\times 2000$. Arrows identify univalents. Figs. 1-12. *Sedum glaucophyllum*. Figs. 1, 2. U788, $n=14$. Fig. 3. U785, $n=22$. Fig. 4. U515, $n=28$. Fig. 5. U575, $n=21_{II}+1_I$. Fig. 6. U560, $n=22_{II}+1_I+5_I$. Fig. 9. Figs. 7, 8. U451, $n=17_{II}$ U549, $n=19_{II}+3_I$. Figs. 10, 11. U787A, $n=15_{II}+5_I$ (1 large and 4 small univalents. One bivalent slightly out of focus at right in Fig. 11). Fig. 12. U787A, Anaphase I, with 4 of 5 lagging univalents in focus and dividing equationally. Fig. 13. U1672. *S. nevii*, $n=6$. Fig. 14. U751, *S. ternatum*, $n=8$. Fig. 15. U450, *S. ternatum*, $n=16$, with some secondary associations (top, lower center and right). Fig. 16. U1128, *S. pulchellum*, $n=11$.



sistently had 21 bivalents and a small univalent at metaphase I (Fig. 5), and is considered to represent a monosomic ($2n-1$) plant. In two other collections (U560, U767) an extra unpaired chromosome was seen in some cells (Fig. 6). In other cells it presumably contributed to the formation of a trivalent, though this could not be identified. These plants are considered to be trisomics ($2n+1$) for one of the smaller chromosomes in the set.

The most interesting cytological variants are some apparent descendants of natural hybrids between the 14- and 22-chromosome races, collected in three different years at the south end of a limestone bluff along the North Fork of the Shenandoah River near Woodstock, Virginia (U451, U549, U787A). Seven other plants (U787B-H), spaced 40 to 150 yards apart to the north along the bluff, all had $n=14$. The closest plant (U787B), 40 yards north, had chromosome bridges in many cells at anaphase I, suggesting that it was heterozygous for an inversion that may have been introduced by the hybridization. The closest other population known to this had $n=22$ (U763). It was found about 9 miles west, or 16 miles upstream by way of the river and its tributary, Stony Creek.

Four of these putative hybrids have been studied cytologically and no two of them are the same. Exact interpretations are difficult, but the first collection (U451) included two different cytological types. One most often had 14 bivalents and 3 univalents at metaphase I and probably resulted from a backcross of a hybrid to the 14-chromosome race. The other was most often interpreted as forming 17 bivalents and 5 univalents, including 3 very small ones, at metaphase I (Figs. 7, 8). This plant is considered to have resulted from a backcross of the hybrid to the other, 22-chromosome parent. Still another plant (U549) was interpreted as having 19 bivalents and 3 univalents, including 2 small ones and a slightly larger metacentric (Fig. 9). This apparently resulted from a different backcross to the 22-chromosome parent.

The fourth putative hybrid (U787A) apparently formed

15 bivalents and 5 univalents, including 4 small ones and a large one, at metaphase I (Figs. 10-11). Such a plant could arise theoretically by union of a gamete bearing $14 + p$ chromosomes with another bearing $14 + q$ chromosomes, where $p + q = 7$ and includes two chromosomes that pair with each other and 5 more that do not. Gametes of these types would be expected from an F_1 hybrid between the 14- and the 22-chromosome races, or from certain of its later-generation progeny. In this hybrid (U787A), anaphase I usually showed 5 laggards, one of them large, as would be expected from the usual number of univalents (Fig. 12).

Although no plant studied was considered to be an F_1 hybrid, from the plants that were studied it seems likely that spores and gametes produced by the F_1 must bear various chromosome numbers between 14 and 22. This implies that pairing in the F_1 brings 14 of the chromosomes from the 22-chromosome parent into association with the 14 chromosomes of the other race, and the remaining 8 chromosomes are distributed more or less at random, either because they enter into the formation of multivalents or because they fail to pair and remain as univalents. Conceivably, this unstable cytological situation might eventually evolve a stable race with still another chromosome number. In fact, it may offer clues to the origin of the 22-chromosome race, e.g., from the progeny of a fertile triploid of the 14-chromosome race.

Morphologically all three chromosome races are very similar and clearly would be assigned to the same species. Detailed studies of *Sedum glaucophyllum* are being made by my colleague, Professor R. T. Clausen. His work should reveal whether any consistent morphological distinctions can be made among the chromosome races.

Several other small species of *Sedum* of eastern United States also have 4-parted, more or less white flowers and have often been confused with *S. glaucophyllum*. Besides *S. nevii*, these include particularly *S. ternatum* and *S. pulchellum*. Cytologically these are all distinct from each other and from *S. glaucophyllum*.

Clausen (1949) reported that true *S. nevii* was known at only three localities, two in Alabama and one in southeastern Tennessee. During these studies a fourth locality was discovered on rocks along the east side of the Chattahoochee River below Goat Rock Dam, above Columbus, Georgia (U339, U624). I believe this is the first record of the species from Georgia. Meiotic chromosomes of the species appear similar at all four localities, with none of the 6 bivalents consistently distinctive or showing the elongate form of the large bivalents in *S. glaucophyllum*.

Although *S. ternatum* now is more widely distributed, it probably is native only from southern Pennsylvania to Indiana and Alabama. Baldwin (1942) has published a map showing the distribution of 71 plants with $2n = 16, 24$ (triploid), 32 and 48. Throughout most of its range only the tetraploid ($n=16, 2n=32$) was found. Diploid plants ($n=8, 2n=16$) were restricted to a rather narrow belt about 150 miles long on both sides of the border of Virginia with West Virginia and Kentucky, an area in which tetraploids also occurred. The only hexaploid ($2n=48$) was from Alabama, where otherwise only tetraploids were found.

In connection with the present work, chromosomes of 81 more collections of *S. ternatum* were studied, including 15 diploids ($n=8$, Fig. 14), 2 triploids, and 64 tetraploids ($n=16$, Fig. 15). These extend the known range of the diploid 100 miles farther to the northeast (Fig. 17), but otherwise conform closely to the distribution of the chromosomal strains reported by Baldwin. The similarity in morphology between diploid and tetraploid *S. ternatum* and the occurrence of multivalents at meiosis in the tetraploid led Baldwin (1936) to suggest that it is an autotetraploid. Once again, the present study supports Baldwin's conclusions. Metaphase I figures (Fig. 15) usually include close secondary associations, multivalents and occasionally univalents, and some metaphase II plates show as few as 13 or as many as 19 elements, due to unequal distribution during anaphase I.

Baldwin (1944) suggested that 14-chromosome *S. glauco-*

phyllum (which was the only form he knew, and which he called *S. beyrichianum*, the correct name being not yet available) arose by amphidiploidy between true *S. nevii* ($n=6$, Fig. 13) and diploid *S. ternatum* ($n=8$, Fig. 14). *S. ternatum* has much broader leaves than *S. glaucophyllum*, and they are generally in whorls of 3. Although *S. glaucophyllum* is more like *S. nevii*, it differs somewhat in the direction of *S. ternatum* (Clausen, 1949). This can be construed as supporting Baldwin's hypothesis of an amphidiploid origin for *S. glaucophyllum*.

The next question concerns the origin of the 8 chromosomes by which the two principal races of *S. glaucophyllum* differ. In this regard, Baldwin's suggestion leads to an obvious second theoretical possibility: that the 22-chromosome strain of *S. glaucophyllum* may have arisen in similar fashion, either by a second amphiploidy between 14-chromosome *S. glaucophyllum* and diploid *S. ternatum* ($n=8$) or directly between *S. nevii* ($n=6$) and tetraploid *S. ternatum* ($n=16$, Fig. 15). In either case, the 22-chromosome strain of *S. glaucophyllum* would be an autoallopolyploid (NNTTTT), since it would bear two sets of chromosomes from *S. ternatum* (T) for each one of *S. nevii* (N). It would therefore be expected to resemble the former more closely than the latter. This is not the case.

Multivalents are common in tetraploid *S. ternatum*, but in 22-chromosome *S. glaucophyllum* they are not ordinarily seen. Also, in the putative descendants of hybrids between the 14- and 22-chromosome races of *S. glaucophyllum* the extra chromosomes presumably represent some of the 8 chromosomes by which the races differ. However, these seem to show little or no tendency to enter into multivalent formation, as might be expected if they had 8 homologues (or homoeologues) in the complement of 14-chromosome *S. glaucophyllum*.

The 8 chromosomes by which the two principal races of *S. glaucophyllum* differ are mostly small and not distinctive. The hypotheses of amphiploidy hold that these chromosomes must have come from *S. ternatum*. However, although there

is some range in size among the chromosomes of *S. nevii* and *S. ternatum* (Figs. 13, 14), neither species is characterized by any meiotic bivalents as distinctive as the longest ones in *S. glaucophyllum*. (Compare also figures of somatic and meiotic chromosomes in the three species in Baldwin, 1936, 1942a).

Since the large, distinctive chromosomes of *S. glaucophyllum* occur in all collections of all races, either their origin must have coincided closely with that of the species or they must have been introduced from some ancestral species. But no other species of eastern North America has chromosomes that look like these. Thus, if *S. glaucophyllum* arose as an amphidiploid, as proposed by Baldwin (1944), it is not a simple, straightforward case.

The chromosome numbers are compatible with the hypotheses of amphiploidy, but the form and behavior of the chromosomes and the morphology of the plants do not fit very well. Some repatterning of the karyotype, mostly by translocations, would also be required at about the same time to account for the long chromosomes of *S. glaucophyllum*. Probably some rebalancing of the genotype also would be necessary to account for the closer resemblance of all chromosome races to *S. nevii* rather than to *S. ternatum*. Determinations of the amounts of DNA that characterize the chromosome complements of these various species and races should provide a good test of the hypotheses of amphiploidy.

In 1948, Dr. Robert E. Lee, of Cornell, produced an artificial hybrid between 14-chromosome *S. glaucophyllum* (Clausen 6795) and *S. nevii* ($n=6$). My slides of this are not good enough for a definitive cytological analysis, but somatic metaphases in anther walls have about the 20 chromosomes expected. Meiotic metaphase I has about 8 to 12 elements, including some large and complicated multivalents and a variable number of univalents. The simplest interpretation of the multivalents is that in some cases a chromosome of *S. nevii* synapses at different places along

its length with two or more chromosomes of *S. glaucophyllum*.

The range of *S. ternatum* today includes most of the range of *S. nevii* and all the range of *S. glaucophyllum*, but the last two species are separated by a gap of 250 miles. Opportunities for natural hybridization may have been offered during cooler, glacial times, when presumably more southerly distributions prevailed.

Sedum glaucophyllum and *S. ternatum* were found together at 11 localities. Tetraploid *S. ternatum* ($n=16$) was found with the 14-chromosome strain of *S. glaucophyllum* at five places, with the 22-chromosome strain at four, and with the 28-chromosome strain at one. Triploid *S. ternatum* ($2n=3x=24$), which probably implies the presence of the diploid nearby, was found once with 22-chromosome *S. glaucophyllum*. Although the range of *S. glaucophyllum* overlaps much of the range of diploid *S. ternatum*, the two were never found together. Possibly it is worth looking for localities where both diploid *S. ternatum* ($n=8$) and *S. glaucophyllum* occur together, and, if they are found, to determine whether both species are stable there.

The mostly winter-annual species, *S. pulchellum*, especially in its juvenile form, is very similar to *S. nevii* and *S. glaucophyllum* (Clausen, 1949). To the south, distribution of *S. pulchellum* overlaps that of *S. nevii*, but it is separated from *S. glaucophyllum* by about 150 miles at the closest. Baldwin (1943) mapped the distribution of 45 collections of *S. pulchellum*, representing diploid ($n=11$), tetraploid ($n=22$) and hexaploid ($n=33$) chromosome races. The 12 additional collections of this species that I have studied represent all 3 chromosome races and conform in distribution to Baldwin's map. The 22-chromosome (tetraploid) race of *S. pulchellum* lacks the distinctive large chromosomes of the 22-chromosome race of *S. glaucophyllum*. Their chromosome numbers and karyotypes must have evolved in different ways, and their similarity in number is merely coincidence.

ECOLOGICAL OBSERVATIONS

Efforts to correlate the distribution of the chromosome races of *S. glaucophyllum* with the geology and with the drainage history of the area have so far not been very productive. Much of the range of the species is an area of long, parallel anticlinal and synclinal ridges and valleys. It has a history of stream piracy as the headwaters of streams that flow more directly eastward, notably the James and Roanoke Rivers, have captured tributaries from streams with longer courses, notably the New and Potomac Rivers (Wright, 1934).

No clear correlation of distribution with drainage is apparent. The greatest concentration of the 22-chromosome race is in, or on the borders of, the James River drainage, where 68 of its 81 localities occur (Fig. 17). However, 18 of the 65 localities of the 14-chromosome race also are in the James basin, 12 of them in its southern part, which may earlier have belonged to New River drainage (Wright, 1934). But five of them, and the four localities of the 28-chromosome strain, are in the heart of the James River drainage, near or along its tributary, the Cowpasture River. In regions contiguous to the James River basin, the 22-chromosome race was found to the west at 7 localities in West Virginia in drainage of the Greenbrier River, a tributary of the lower part of the New River, and to the northeast at two localities in drainage of the Middle River, an upper tributary of the South Fork of the Shenandoah. The only really disjunct localities of the 22-chromosome race are 3 near the North Fork of the Potomac River, southwest of Cumberland, Maryland, and one in western Shenandoah County on Stony Creek, a tributary of the North Fork, Shenandoah River.

The 14-chromosome race of *S. glaucophyllum* is more widely distributed, especially in the north, where it predominates, and in the south, where the 22-chromosome race is unknown. Forty-seven of its 65 localities are outside the James River drainage, 19 to the south and south-

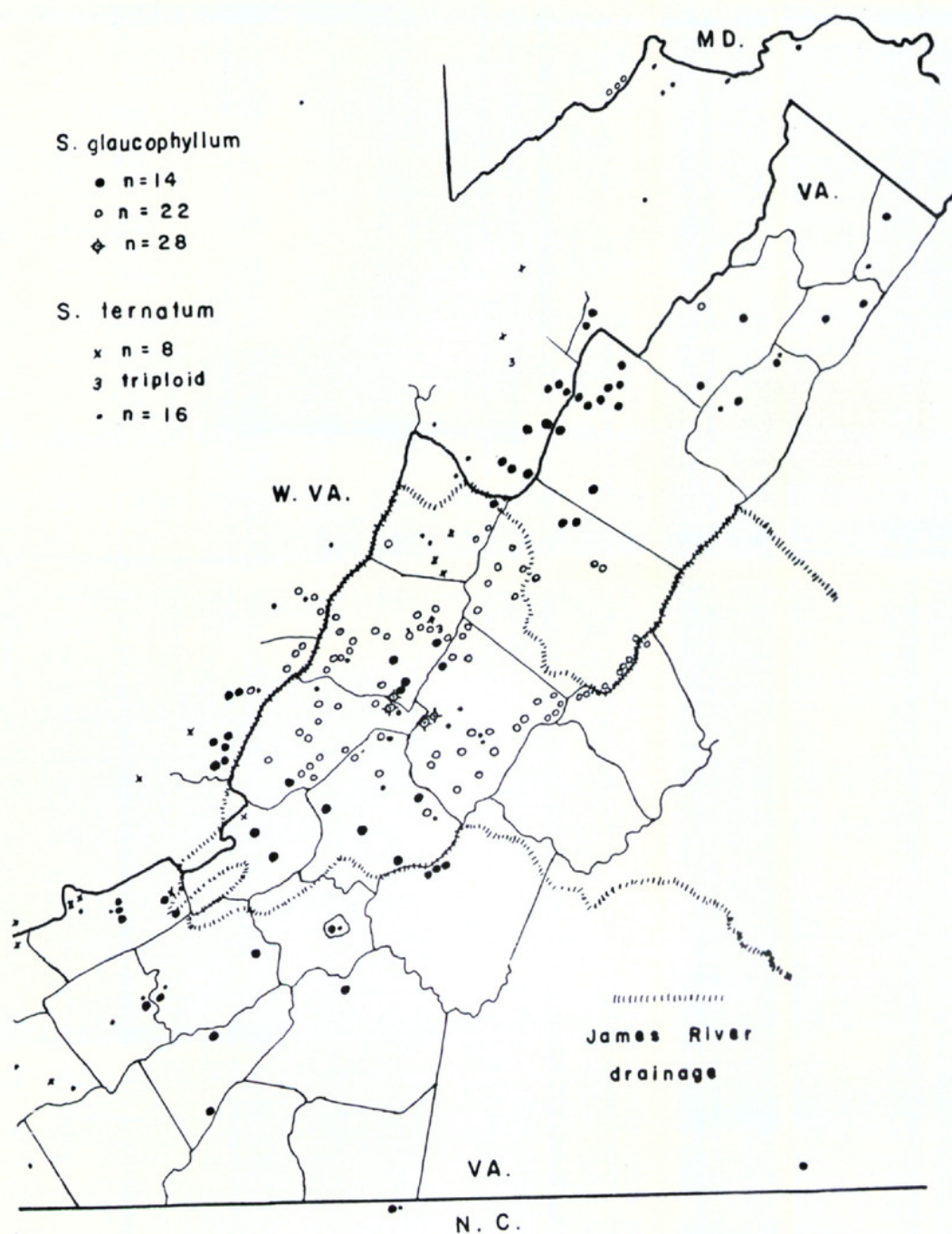


Fig. 17. Distribution of chromosome races of *Sedum glaucophyllum* and *S. ternatum* in western Virginia and adjacent regions. Three localities for *S. glaucophyllum* are from Baldwin (1942a). Localities for *S. ternatum* are from Baldwin (1942b) and Uhl (unpublished).

west, and 28 to the north. It occurs sporadically along the crest of the Blue Ridge, from Rocky Knob (Floyd Co.) north to Peaks of Otter (Bedford Co.). Farther north, the crest of the Blue Ridge bears the 22-chromosome race from east of Lexington to near Waynesboro.

At several places the two races occur within a few miles of each other, sometimes in the same stream valley. Thus, the upper valley of Anthony Creek, north of White Sulphur Springs, West Virginia, is occupied by the 22-chromosome race (U573, U574, U575, U577) for more than 10 miles; then, farther down, where the stream begins to cut through Hopkins Mountain, and separated by an interval of no more than 2 miles, the 14-chromosome race occurs (U578, U579). On the Cowpasture River at Millboro Springs, Bath Co., the 14-chromosome race (U472) is only 4 miles south of two localities of the 22-chromosome race farther upstream (U772, U774), and 5 miles west of it at Panther Gap (U330). Nearby, along Bratton Creek, southwest of Goshen, collections of the 14- and 22-chromosome races (U779, U780) are separated by only 2.3 miles in what appears from the topographic map (Millboro 15' sheet, USGS) to be the same stratigraphic situation. These last two cases appear to be on the boundary between a pocket where the 14- and 28-chromosome races are surrounded by the 22-chromosome race (Fig. 17).

In the valley of Potts Creek, southwest of Covington, Virginia, again with apparently the same stratigraphy, the 14-chromosome race (U596) is separated from the 22-chromosome race (U595) by only 5 miles. In Botetourt Co., Virginia, between Buchanan and Natural Bridge, no more than 4 miles separate the 14-chromosome (U510) and 22-chromosome (U508) races. Doubtless some of these intervals could be reduced by further collecting, and the areas may be worth searching for possible hybrids between the two races.

The occurrence of *S. glaucophyllum* seems clearly related to humidity and to the availability of moisture. At lower elevations it is found chiefly on shady bluffs along streams,

but at higher elevations it occurs in rocky places more generally. Both chromosome races were found most often on shale and limestone, but both occur on quartzitic rock along the crest of the Blue Ridge or even on sandstone. Generally the species is absent from more acid environments.

In elevation, the 14-chromosome race was found from 200 feet, near South Hill, Virginia (*Clausen & Uhl* 6801), to about 3900 feet or more, at the type locality, Mountain Lake, Virginia, with a mean elevation for 47 localities of 1677 feet. The 22-chromosome race ranges from 750 feet, on the Maury River, near Glasgow (U603), to 3320 feet on the Blue Ridge Parkway north of Tye River Gap (U607), with a mean for 80 localities of 1726 feet. The four localities of the 28-chromosome race range from 1150 feet along the Cowpasture River (U326) to 2680 feet on North Mountain (U515), mean 1825 feet. The chromosome races obviously do not differ from each other in their altitudinal distributions.

No effort is made here to relate distribution of the chromosome races with remnants of the ancient Appalachian penepains, the Schooley, the Harrisburg, etc. (Wright, 1934). The species occurs mostly on steep rocky slopes and bluffs. Generally these are young and transient topographic features, but because of recent uplift they are now found at all elevations on the old erosional surfaces. The fact that both chromosome races occur, though at different places, on perhaps the oldest land surface of all, the crest of the Blue Ridge, appears to argue against a relation between age of the land exposure and distribution of the chromosome races.

More likely the true centers of concentration of the species are at higher elevations along the ridges, where there are fewer roads and where fewer collections were made. Populations on stream bluffs at lower elevations probably originated from these. A better view of distribution of the chromosome races might therefore be based on ridges, rather than on drainage basins. However, except for the Blue Ridge, because of the Parkway, not enough collections

have been made on the ridges to test this idea. Perhaps the valleys cited above, where two chromosome races occur close together, lie between ridges that bear the different races.

Soil with 11 collections of the 14-chromosome strain of *S. glaucophyllum* ranged in pH from 5.65 to 7.75, with a mean of 6.84. For 40 collections of the 22-chromosome strain, the range was pH 5.25 to 8.0, with a mean of 6.54. With so much overlap, the difference of only pH 0.3 in the averages seems not significant. For *S. ternatum* in the same area, soil with 3 diploids ($n=8$) ranged from pH 6.0 to 7.4, mean 6.62; for 8 tetraploids ($n=16$), the range was 6.4 to 7.55, the mean 6.91. These values also do not seem significantly different from each other or from those for *S. glaucophyllum*.

Thus no simple differences in their ecology have been found between the 14- and the 22-chromosome races. Both occupy the same sort of habitat and exhibit the same preferences and tolerances with respect to substrate, acidity and elevation. Probably they compete with each other.

Whatever its origin, because of its chromosome number the 22-chromosome race of *S. glaucophyllum* must have appeared later than the 14-chromosome race. Thus the fact that the former predominates in the heart of the range of the species as a whole suggests that it may have largely replaced the 14-chromosome race there. The 14-chromosome race is mostly peripheral in its distribution, supporting the conclusion that it is older. An experiment to test the survival of the two races in competition with each other under various conditions might give interesting results.

SUMMARY

Study of 180 plants of *Sedum glaucophyllum* from 150 localities reveals chromosome races with $n=14$, $n=22$, and $n=28$. All races have several distinctive bivalents that are longer than any known in other American species. Apparent hybrids between the 14- and 22-chromosome races were

found at one locality. The race with $n=28$ is a local autotetraploid derived from $n=14$.

Baldwin's hypothesis that *S. glaucophyllum* with $n=14$ originated as an amphidiploid between *S. nevii* ($n=6$) and diploid *S. ternatum* ($n=8$) leads to a suggestion that a second amphiploidy, between plants with $n=14$ and $n=8$, may have produced the race with $n=22$. These hypotheses are in good accord with the chromosome number, but chromosome morphology and behavior and the morphology of the plants do not fit well. Some restructuring of the karyotype and rebalancing of the genotype would also be necessary.

The chromosome races of *S. glaucophyllum* do not differ significantly in their tolerances or preferences in substrate, pH, elevation, or general habitat. However, predominance of the 22-chromosome race in the center of the range gives the impression that it has been replacing the 14-chromosome race there.

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Table 1. Collections of *Sedum glaucophyllum*
Studied and Their Chromosome Numbers.

Maryland. ALLEGANY COUNTY: U749 Fort Hill, 0.4 mi. w. of Rawlings, on bluff, 770' ($n=22$); U748, R. T. Clausen 7012 Potomac River bluff, 0.5 mi. s. of Rawlings, 790' ($n=22$); U750 Bluff at SW end of Fort Hill, 4 mi. NE of McCoole, 760' ($n=22$).

West Virginia. HARDY COUNTY: U649 Moorefield River, 2.5 mi. s. of Bass ($n=14$); U648 Moorefield River, 5.7 mi. s. of Bass ($n=14$). PENDLETON COUNTY: U755 $7\frac{1}{2}$ mi. E. of Fort Seybert, 2.1 mi. W. of Sand Spring Gap, 2595' ($n=14$); U647 Rough Run, 4 mi. E. of Fort Seybert ($n=14$); U646 Fisher Run, $1\frac{1}{2}$ mi. NE. of Fort Seybert, 1500' ($n=14$); R. T. Clausen 47-118 Shenandoah Mt., summit ($n=14$); U645 Moorefield River, 2.9 mi. s. of Brandywine, 1650' ($n=14$); U553 5.3 mi. E. of Sugar Grove, 2900' ($n=14$); U644 1.3 mi. NW of Sugar Grove, 2500' ($n=14$); U554 Moorefield River, 0.6 mi. s. of Sugar Grove, ($n=14$). POCAHONTAS COUNTY: U522, U572 Laurel Creek, near Rimel, 2400' ($n=22$); U641 Knapp Creek, 0.8 mi. SE of Huntersville ($n=22$); U570 Knapp Creek, $1\frac{1}{2}$ mi. NW of Huntersville, 2250' ($n=22$). GREENBRIER COUNTY: U573 Anthony Creek, 3.2 mi. s. of Pocahontas County line, 2200' ($n=22$); U574 Anthony Creek, 5.3 mi. s. of Pocahontas County line, 2150' ($n=22$); U575 Anthony Creek, 9.3 mi. s. of Pocahontas County line, 0.7 mi. NE of Neola, 2045' ($n=21+1$); U577 Anthony Creek, 0.5 mi. NW of Camp Wood and 1 mi. NW of Alvon, 1950' ($n=22$); U578 Anthony Creek, at Blue Bend Park, 2.5 mi. w. of Camp Wood, 1945' ($n=14$); U579 Anthony Creek Gorge, 2.2 mi. NE of Anthony, 1870' ($n=14$); U580 Wades Creek, 1.1 mi. E. of White Sulphur Springs, 1920' ($n=14$); U291 Near summit of Kates Mountain, s. of White Sulphur Springs (H. D. Bennett), $3000' \pm$ ($n=14$); U640 Dry Creek, 2.9 mi. SE of White Sulphur Springs, 1975' ($n=14$); U639 Dry Creek, 6 mi. s. of White Sulphur Springs, 2125' ($n=14$); U638 Tuckahoe Run, 7.5 mi. s. of White Sulphur Springs, 2250' ($n=14$).

Virginia. CLARKE COUNTY: Boyce (Baldwin, 1942) ($n=14$). WARREN COUNTY: U788 Shenandoah River, 8 mi. ENE Front Royal, 480' ($n=14$); U547 Lime sink $1\frac{1}{2}$ mi. SW of Front Royal, 560' ($n=14$). SHENANDOAH COUNTY: U451, U549, U787A N. Fork, Shenandoah River opposite junction of Narrow Passage Cr., 3 mi. SW of Woodstock, 765' (Irregular); U787B, C, D, E, F, G, H (7 plants) Same locality ($n=14$); U763 Stony Cr. bluff, 1.3 mi. E. of Liberty Furnace, 1040' ($n=22$); U1669 N. Fork, Shenandoah River, 5 mi. N. of New Market, 920' ($n=14$). PAGE COUNTY: R. T. Clausen 6747A, B, C, D,

E, F, G, H (8 plants) on limestone, near Rileyville ($n=14$); U550 S. Fork, Shenandoah River, 5 mi. SW of Luray ($n=14$). ROCKINGHAM COUNTY: U760 German River, 4.4 mi. N. of Fulks Run, 1280' ($n=14$); U332 German River, just N. of Fulks Run, 1200' ($n=14$); U764 Shoemaker River, 3.0 mi. S. of Genoa, 1240' ($n=14$); U759 Little Dry River, 3.2 mi. W. of Fulks Run, 1360' ($n=14$); U758 Little Dry River, 6.1 mi. W. of Fulks Run, 1560' ($n=14$); U757 7.8 mi. W. of Fulks Run, 4.9 mi. E. of Sand Spring Gap, 1800' ($n=14$); U756 1.9 mi. E. of Sand Spring Gap, 2925' ($n=14$); U765 Dry River, 2.9 mi. W. of Hinton, 1460' ($n=14$); *R. T. Clausen* 6992 Shenandoah Mt., near Summit, 3470' ($n=14$). AUGUSTA COUNTY: U552 Natural Chimneys, 0.7 mi. N. of Mt. Solon, 1380' ($n=14$); U766 1.5 mi. W. of Mt. Solon, 1400' ($n=14$); U767 Middle River, 2.4 mi. N. of Verona, 1280' ($n=22+1$); U610 Middle River, 3.2 mi. N. of Verona, 1360' ($n=22$); U768 E. side, Crawford Mt., 3.6 mi. NW Buffalo Gap, 2520' ($n=22$); U769 W. side, Crawford Mt., 4.8 mi. W. of Buffalo Gap, 2360' ($n=22$); U565 Calfpasture River, 1.0 mi. S. of Lebanon, 1875' ($n=22$); U564 Calfpasture River, 2.8 mi. NE of Deerfield, 1750' ($n=22$); U563 Calfpasture River, 2.1 mi. S. of Deerfield, 1650' ($n=22$); U770 Great North Mt., 6.4 mi. SE of Deerfield, 2560' ($n=22$); U562 Calfpasture River, 1.8 mi. S. of Marble Valley, 1580' ($n=22$); U609 Humpback Gap, Mile 6, Blue Ridge Parkway, 2375' (Nelson County) ($n=22$); U531 Humpback Rocks, S. of Mile 6, Blue Ridge Parkway, 2200' ($n=22$); U530 Ravens Roost, Mile 10.7, Blue Ridge Parkway, 2900' ($n=22$); U225, U529 W. of Laurel Springs Gap, Mile 11.3, Blue Ridge Parkway, 3000' ($n=22$); U224 Mile 13, Blue Ridge Parkway ($n=22$); U528 Mile 16.3, Blue Ridge Parkway (Nelson County), 2700' ($n=22$); U608 2.4 mi. W. of Love, Mile 18, Blue Ridge Parkway, 2700' ($n=22$). NELSON COUNTY: U214, C47-98 6 mi. NE of Tye River Gap, Mile 21, Blue Ridge Parkway ($n=22$); U607 2.4 mi. N. of Tye River Gap, Mile 24.8, Blue Ridge Parkway, 3320' ($n=22$); U527 1.3 mi. N. of Tye River Gap, Mile 25.9, Blue Ridge Parkway, 3175' ($n=22$). HIGHLAND COUNTY: U555 Moorefield River at Palo Alto, 0.3 mi. S. of W. Va. line, 2160' ($n=14$); U525, U566 Shenandoah Mt. summit, on Confederate earthworks, 9.8 mi. E. of McDowell, 2950' ($n=22$); U567 0.4 mi. S. of Headwaters, 2050' ($n=22$); U523 Townsman Draft, near Back Creek, 3.9 mi. SW of Mill Gap, 2300' ($n=22$). ROCKBRIDGE COUNTY: U606 6.6 mi. S. of Tye River Gap, Mile 33.8, Blue Ridge Parkway, 3250' ($n=22$); U526 1.7 mi. NE of Irish Gap, Mile 35.7, Blue Ridge Parkway, 2800' ($n=22$); U605 1.2 mi. E. of Irish Gap, Mile 36.2, Blue Ridge Parkway, 2650' ($n=22$); U621, U786 Little Marys Creek, 0.8 mi. E. of Vesuvius, 1550' ($n=22$); U785 South River, 3.8 mi. SW of Vesuvius, 1250' ($n=22$); U784 South River at bridge, 1.5 mi. NE of Cornwall, 1050' ($n=22$); U783 South River at Cornwall, 1025' ($n=22$); U782 South River at gaging

sta., 4.5 mi. E. of Lexington, 920' ($n=22$); U604 Maury River, w. side of Buena Vista, 875' ($n=22$); U449 E. of US 11 Highway bridge, N. side of Lexington, 900' ($n=22$); U864, U1635 5 mi. s. of Lexington, 1030' ($n=22$); U603 Maury River, E. of Lone Jack Quarry, 2½ mi. NW of Glasgow, 750' ($n=22$); U602 Cedar Creek at Gilmore Mills, ca. 1 mi. below Natural Bridge, 760' ($n=22$); U512 s. Buffalo Creek, ca. 8 mi. SW of Murat, 1200' ($n=22$); U511 s. Buffalo Creek, ca. 8.3 mi. SW of Murat, 1220' ($n=22$); U561 Calfpasture River, 0.6 mi. s. of Augusta County line, 1530' ($n=22$); U560 Calfpasture River, 6 mi. N. of Goshen, 1480' ($n=22$); U781 Calfpasture (=Maury) River, Goshen Pass, 1225' ($n=22$); U780 Bratton Creek, 2 mi. SW of Goshen, 1410' ($n=22$); U779 Bratton Creek, 4.3 mi. SW of Goshen, 1500' ($n=14$); U515 North Mountain, 6.0 mi. W. of Collierstown, 2680' ($n=28$); U514 North Mountain, E. side, 5.1 mi. W. of Collierstown, 2320' ($n=28$). BATH COUNTY: U330 Mill Creek, Panther Gap, 3 mi. W. of Goshen, 1560' ($n=22$); U559 Cowpasture River, ½ mi. E. of Fort Lewis, 6½ mi. s. of Williamsville, 1540' ($n=22$); U775 Dry Run, 7 mi. NW of Millboro Springs, 1480' ($n=22$); U772 Blackie's Hollow, 4 mi. directly N. of Millboro Springs, 1460' ($n=22$); U774 Cowpasture River, 0.2 mi. W. of U772, 1380' ($n=22$); U777 Thompson Creek, 4.7 mi. NW of Millboro Springs, 1410' ($n=22$); U472 Cowpasture River, s. edge of Millboro Springs, 1350' ($n=14$); U328 Cowpasture River, 10 mi. NE of Clifton Forge, 1175' ($n=14$); U471 Cowpasture River, 9 mi. NE of Clifton Forge, 1150' ($n=14$); U518 Mill Creek, 7.9 mi. N. of dam at Douthat Lake, 1450' ($n=14$); U517 Wilson Creek, below dam at Douthat State Park, 1420' ($n=22$); U519 E. of summit of Warm Springs Mt., 1.8 mi. E. of Warm Springs, 2875' ($n=22$); *R. T. Clausen* 6991 West of Warm Springs ($n=22$); U520, U586 Back Creek, 1.5 mi. s. of Mountain Grove, 1750' ($n=22$); U521 Little Back Creek, 3.3 mi. NW of Mountain Grove, 1860' ($n=22$); U587 N. entrance of Richardson Gorge, Jackson River, 6.8 mi. W. of Warm Springs, 1680' ($n=22$); U588 SE end Richardson Gorge, Jackson River, opposite junction of Back Creek, 1700' ($n=22$); U589 Jackson River, 3.5 mi. s. of junction of Back Creek, 1560' ($n=22$); U585 Bolar Draft, 7½ mi. s. of Mountain Grove, 1640' ($n=22$); U584 Jackson River, 2.6 mi. N. of Alleghany County line, 1530' ($n=22$). ALLEGHANY COUNTY: U470 Cowpasture River, 6 mi. NE of Clifton Forge, 1160' ($n=28$); U326, U423 Cowpasture River, 5½ mi. NE of Clifton Forge, 1150' ($n=28$); U516 Wilson Creek, 4½ mi. N. of Clifton Forge, 1200' ($n=22$); U422 Johnson Mt., 4 mi. s. of Lowmoor, 1875' ($n=22$); U268 Road cut, US220, 8 mi. NNE of Covington, 2250' ($n=22$, $n=44$); U583 Jackson River, at W. end of The Gorge, 1 mi. s. of Bath County line, 1500' ($n=22$); U591 Jackson River, 0.2 mi. s. of Indian Draft, 6 mi. N. of Covington, 1350' ($n=22$); U597 Blue Spring Creek, 7 mi. directly s.

of Covington, 1750' ($n=22$); U325 Dunlap Creek, 3 mi. w. of Covington, 1325' ($n=22$); U581 Cove Run, 1.6 mi. N. of Callaghan, 1520' ($n=22$); U592 Potts Creek, 3.6 mi. s. of Covington, 1230' ($n=22$); U593 Potts Creek, 7.3 mi. SW of Covington, 1300' ($n=22$); U595 Potts Creek, 10.9 mi. SW of Covington, 1350' ($n=22$); U596 Potts Creek, 16.7 mi. SW of Covington, 3.4 mi. SW of Jordan Mines, 1600' ($n=14$); U324 3 mi. NE of Crows, 1575' ($n=22$). BOTETOURT COUNTY: U469 James River, 2 mi. s. of Iron Gate, 1000' ($n=22$); U421, U598 Richpatch Mountain, 7 mi. s. of Lowmoor, 1800' ($n=22$); U599 Craig Creek, 2.3 mi. NW of Eagle Rock, 950' ($n=22$); U510 Renick Run, 7 mi. N. of Buchanan, 1570' ($n=14$); U508, U601 0.7 mi. NW of Indian Rock, 1000' ($n=22$); U420 Craig Creek, 2 mi. SW of Oriskany, 1175' ($n=14$); U600, *R. T. Clausen* and *C. H. Uhl* 6795 Catawba Creek, 1.4 mi. N. of Fincastle, 1050' ($n=14$); U1585 Pine Tree Overlook, Mile 95.3, Blue Ridge Parkway, 2524' ($n=14$). BEDFORD COUNTY: *R. T. Clausen* & *Uhl* 6785 Spring in notch between Peaks of Otter, 2360' ($n=14$); *R. T. Clausen* & *Uhl* 6792 South Peak of Otter, elev. ca. 3100' ($n=14$); *R. T. Clausen* & *Uhl* 6789 South Peak of Otter, elev. ca. 3400' ($n=14$). CRAIG COUNTY: U322 Potts Mountain summit, 5 mi. SE of Paint Bank, 3450' ($n=14$); U321 Meadow Creek, 2.4 mi. SW of Newcastle, 2100' ($n=14$). GILES COUNTY: U429 Sinking Creek, Mouth of Tauney's Cave, 1½ mi. NE of Maybrook, (*D. W. Bierhorst*) ($n=14$); Mountain Lake (*J. T. Baldwin*, 1942) ($n=14$); U320 New River, 1½ mi. N. of Ripplemead, 1700' ($n=14$); U636 New River, 0.5 mi. s. of Ripplemead ($n=14$); U430 New River, 0.7 mi. s. of Ripplemead, 1875' (*D. W. Bierhorst*) ($n=14$). ROANOKE COUNTY: Roanoke, (*J. T. Baldwin*, 1942) ($n=14$). MONTGOMERY COUNTY: U1120 Roanoke River, w. of Elliston ($n=14$); U463 Little River, ½ mi. s. of Claytor L. dam, 1775' ($n=14$). PULASKI COUNTY: U465 New River, at Claytor L. dam ($n=14$). FRANKLIN COUNTY: U1668 Maggoodee Creek, N. of Boones Mill, 1050' ($n=14$). FLOYD COUNTY: U462 Little Camp Creek, 10 mi. NW of Floyd ($n=14$); U461 Rocky Knob Park campground, Mile 169, Blue Ridge Parkway, 2250' ($n=14$). MECKLENBURG COUNTY: *R. T. Clausen* & *Uhl* 6801 Goodes Ferry, Roanoke River, US1, s. of South Hill, 200' ($n=14$).

North Carolina. ROCKINGHAM COUNTY: *R. T. Clausen* 6763 Smith River, near Spray (Eden), 650' ($n=14$).



Uhl, Charles Harrison. 1970. "HETEROPLOIDY IN SEDUM GLAUCOPHYLLUM." *Rhodora* 72, 460–479.

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