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CHROMOSOMES OF *VILLADIA* AND *ALTAMIRANOA* (CRASSULACEAE)[1]

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Villadia, ranging from Texas to Peru with some 25 species, has a rather distinctive thyrsoid to spicate inflorescence, and we keep it as a genus separate from *Sedum.* Twenty species show every gametic chromosome number from 9 to 17 and also 20–22 and higher. Chromosome pairing in hybrids shows that the species differ by many translocations and that species with 21 or lower are effectively diploid. More specialized species tend to have fewer and larger chromosomes, suggesting that through time translocations have rearranged the ancestral genome into fewer units. We suspect that relocated genes may be programmed differently, affecting phenotype. Thus *Villadia* is like *Echeveria* in having a remarkably long descending series of evidently diploid chromosome numbers. *Altamiranoa,* often included in *Villadia,* with about 15 species from Mexico south, more closely resembles *Sedum* in its broadly cymose inflorescence. It appears polyphyletic, with no clear boundary from *Sedum,* and we disperse its species in *Sedum.* The ten species studied have gametic numbers from 20 to 29 that probably are effectively diploid, with a few higher and probably polyploid. Again, chromosome pairing in hybrids shows that the species differ by many translocations. Putative relatives in *Sedum* section LEPTOSEDUM have $n = 26$ to 31. Thus cytologically as well as morphologically *Altamiranoa* has remained more similar than *Villadia* to its *Sedum* relatives.

Key words: *Altamiranoa*; chromosomes; dysploidy; hybrids; *Villadia.*

J. N. Rose proposed the genus *Villadia* for 11 Mexican Crassulaceae, eight described as new and three named before in *Cotyledon* (Britton and Rose, 1903, 1905). At the same times he proposed *Altamiranoa* for 12 Mexican species, three described as new and nine formerly in *Cotyledon, Sedum,* or *Umbilicus.* These are all *Sedum*-like plants with petals united at least near the base, but *Villadia* has a narrow thyrse of several few-flowered cincinni, sometimes reduced to a raceme or spike, while *Altamiranoa* has a broad cyme of a few several-flowered cincinni.

In a generic revision of the family, Berger (1930) recognized both genera, adding to *Altamiranoa* eight Peruvian species formerly in *Cotyledon* or *Sedum.* He assigned both genera to his subfamily Echeverioideae, together with other American, and especially Mexican, genera having connate petals, but these two and *Lenophyllum* Rose differ from the rest in having terminal rather than lateral inflorescences. Baehni (1937) and Clausen (1940) combined *Altamiranoa* with *Villadia,* Clausen making it a section; and most authors since then have used *Villadia* in this expanded sense.

Authors generally have agreed on the limits of *Villadia* in the sense of Rose, with its distinctive thyrsoid to spicate inflorescence, but they have disagreed about *Altamiranoa,* which has a broad cymose inflorescence, as usual in *Sedum,* and has no clear boundary from Mexican *Sedum.* In his cladistic tree based on chloroplast DNA, van Ham (1995) had only a few Mexican species and none of *Villadia* proper, but he placed *Villadia* (*Altamiranoa*) *batesii* (which we call *Sedum goldmanii*) closest to *S. bourgaei* Hemsl. of sect. FRUTICISEDUM. Though it is not remarkably different, we believe that in this family of uncertain generic limits *Villadia* can best stand as a genus of its own, apart from *Sedum. Altamiranoa* in the sense of Rose clearly is polyphyletic, and Fröderström (1935) already returned some species to *Sedum*; we now believe that all species of *Altamiranoa* are best dispersed in *Sedum* (Moran, 1996). The present chromosome study adds some support to this treatment.

Although we would formally restrict *Villadia* to Rose's original definition, in this paper we also consider the species of the *Altamiranoa* group, which we refer to *Sedum. Villadia* (sensu stricto) has perhaps 25 species, some not yet named. Most are Mexican, but one extends into the Big Bend region of western Texas and another into Guatemala, and two or three others grow in the Andes of Peru. The *Altamiranoa* group has about seven species in Mexico and others, poorly known, from Peru to Argentina. Chromosome numbers in both groups are very diverse, with a great deal of dysploidy and some polyploidy, and they have been helpful in sorting out the species.

Although natural hybrids among the Mexican Crassulaceae are uncommon, Uhl (1992) has made hybrids that directly or indirectly interconnect more than 200 species of what we would liberally call about nine genera, including both *Villadia* and *Sedum* (with *Altamiranoa*), showing these species to be part of a gigantic comparium. Study of chromosome pairing in these hybrids gives useful information about similarities in the parental genomes, about ploidy, and about the nature of the changes in their chromosomes during evolution.

MATERIALS AND METHODS

Uhl studied plants cytologically as they became available over more than 40 years (Table 1). He fixed buds in three parts chloroform: two parts absolute ethanol: one part glacial acetic acid; and he studied meiotic chromosomes in aceto-carmine squash preparations of pollen moth-

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TABLE 1. Collections studied.

Villadia acuta Moran and C. H. Uhl ($n = 16$)
- San Luis Potosí Type collection. Pico del Agujón, 30 km S of Río Verde toward Mina el Refugio. *M. Kimnach 296 = HNT 16386 = U1278* (Fig. 1).

Villadia albiflora (Hemsl.) Rose ($n = 15$)
- Puebla: Topotype of *V. ramosissima* Rose. Limestone, Mex 150, 9 km N of Tehuacán. *C. H. Uhl 1893.*
- Puebla: San Antonio Texcala, 1850 m. Near 18°24′N; 97°26′W. *R. Moran 6361.*
- Puebla: Cerro de la Yerba, W of San Luis Atolotitlán. *J. Bauml and M. Kimnach 335 = HNT 45399 = U2673.*
- Puebla: Cerro de la Yerba. *R. Moran and M. Kimnach 7722.*
- Oaxaca: Cliff W of Mex 125, 5 km S of Miltepec. *C. H. Uhl 1454* and *1455.*
- Oaxaca: Cliff N of Mex 190 at Km 21.9 SE of Huajuapan de León, 1980 m. *C. H. Uhl 1900.*
- Oaxaca: 29 km SE of Huajuapan de Léon on Mex 190, 1980 m. *M. Kimnach and M. Cházaro 3211B = U3074* and *U3139.*
- Cultivated: *R. T. Clausen 51-14* and *51-15* (Fig. 2).

Villadia aperta Moran and C. H. Uhl ($n = 15$)
- Durango: Type collection. Cliff 4.3 km W of Revolcaderos, Km 192.7 W of Durango, 2075 m. *C. H. Uhl 2255* (Fig. 3).

Villadia aristata Moran ($n = 10$)
- Nuevo Léon: Granite on Mt. Delgadito, near Dulces Nombres, 2600 m. Near 24°00′N; 99°40′W. *A. Lau 073 = HNT 41306 = U2799.*
- San Luis Potosí Isotype. Sierra de Alvarez, on limestone near Km 33 E of San Luis Potosí 2350 m. Near 22 °06′N; 100°41′W. *R. Moran 10006* (Fig. 4); also *C. H. Uhl 1841.*
- San Luis Potosí Near Km 36 on Mex 70. *R. Moran 6323*; *C. H. Uhl 1843* from nearby.
- San Luis Potosí 2 km W of Puerto Altamira summit, 41 km E of San Luis Potosí. *R. Moran and C. H. Uhl 13358.*
- San Luis Potosí 1.8 km S of Puerto Altamira summit toward radiotelephone tower, 2625 m, *R. Moran and C. H. Uhl 13375.*

Villadia cucullata Rose ssp. *cucullata* ($n = 11$)
- Coahuila: S side of Cuesta La Muralla, on limestone ca 1 km N of San Lorenzo Campamento, 74 km S of Monclova, 1220 m. *C. H. Uhl 1515.*
- Coahuila: Rocky bank, W side of canyon, ca 18 km N of Saltillo. *C. H. Uhl 1524.*
- Coahuila: Above W side of Chorro Canyon, 27 km SE of Saltillo. *C. H. Uhl 1498.*
- Coahuila: Puerto Piñones summit, Km 47 S of Saltillo on Zacatecas road. *C. H. Uhl 1518.*
- Cultivated. Collected by Fritz Schwartz. *UCBG 52.361* (Fig. 5).

Villadia cucullata ssp. *apiculata* Moran and C. H. Uhl ($n = 11, 22?$)
- Tamaulipas: 30 km SW of Ciudad Victoria toward Jaumave. *M. Kimnach and G. Lyons 1450 = HNT 28072 = U2076* (Fig. 25). ($n = 21 + 1$).
- San Luis Potosí Type collection. 2.5 km W of Guadalcazar, 1800 m. *R. Moran 6343.*
- Hidalgo: Limestone along trail from Jacala to Escondido. *H. E. Moore Jr. 8039 = U834* (Fig. 6).

Villadia sp. aff. *cucullata* ($n = 10$)
- Querétaro: Limestone E of bridge 8 km NE of Vizarrón toward San Joaquín. *C. H. Uhl 2122* (Fig. 7).

Villadia guatemalensis Rose ($n = 20, 21$)
- Oaxaca: Near Peña Blanca, near end of Huautla road. *J. Bauml and M. Kimnach 446 = U2664.* $n = 21$.
- Oaxaca: Km 65.5 on Mex 190, 3 km E of road to Tlaxiaco, 2375 m. *C. H. Uhl 1908.* $n = 21$.
- Oaxaca: Limestone on Mex 125, 7.8 km toward Tlaxiaco from Mex 190. *W. Handlos 552B = U2094.* $n = 21$.
- Oaxaca: Pine/oak forest, ca Km 50 on Mex 125 S of Mex 190, 6 km N of Tlaxiaco. *W. Handlos 556B = U2097.* $n = 21$.
- Oaxaca: Small side canyon of Tomellín Canyon, Mex 131 at Km 59 N of Telixtlahuaca, 1100 m. *C. H. Uhl 2366.* $n = 21$.
- Oaxaca: 36 km W of Telixtlahuaca, 2285 m. *C. H. Uhl 1904.* Probable triploid.
- Oaxaca: Ca 25 km on Mex 190 NNW of Oaxaca city. *J. Bleck 479 = HNT 21850 = U2055.* $n = 21$ (Fig. 8).
- Oaxaca: Sierra de Juárez, 1.3 km N of Ixtlán, 1940 m. J. Folsom et al. *HNT 53347 = U2832.* $n = 21$.
- Oaxaca: Sierra de Juárez, above Mex 175, 8.6 km N of Mex 190, 1900 m. *C. H. Uhl 2370.* $n = 21$.
- Oaxaca: Ca 8 km E of Mitla, 1875 m. Near 16°55′N; 96°18′W. *R. Moran 6382.* $n = 20$.
- Oaxaca: N of Totolapán. *R. Moran and M. Kimnach 7752.* $n = 20$ (Fig. 9).
- Oaxaca: Sierra de San Felipe. *R. T. Clausen 6073.* $n = 21$.
- Guatemala: Dept. Sololá. N shore of Lake Atitlán, 3 km E of Panajachel, 1620 m. *C. H. Uhl 2604.* $n = 21$.
- Guatemala: Exact locality not known. *Clausen 44-27.* $n = 21$.

Villadia imbricata Rose ($n = 12$)
- Puebla: N of road to Huautla, ca 9 km N of Teotihuacán del Camino, 1900 m. *C. H. Uhl 2872. J. Bauml and M. Kimnach 375 = U2657* from nearby.
- Oaxaca: 7 km W of Concepción Papalo, 1700 m. *M. Kimnach 5309 = U3071.*
- Oaxaca: Ixhuatlan, Tomellín Canyon. *A. Lau 057 = HNT 41303 = U2577.*
- Oaxaca: Side canyon of Tomellín Canyon at Km 50.8 N of Telixtlahuaca, 1550 m. *C. H. Uhl 2368* (Fig. 10).
- Cultivated: Montreal Botanical Garden. *U708* ($n = 12 + 2B$, Fig. 11).
- Cultivated: Said to have come from Río Basura, on road to the Sierra Canela in Chihuahua, but that seems most unlikely for this species. *A. Lau 074 = HNT 41307 = U2580.*

Villadia incarum (Ball) Baehni & J. F. MacBr. ($n = 88–89$)
- Peru: Dept. Lima, Prov. Huarochiri. Río Blanco on Río Rímac, 3500 m. *P. C. Hutchison 582 = UC 52.790.*
- Peru: Dept. Ancash, Prov. Bolognesi: Huasta. Collected by W. Roberts. *R. Moran 18366.*
- Peru: Cultivated. *Clausen 366* and *C42-32* (Fig. 13).

Villadia laxa Moran and C. H. Uhl ($n = 14$)
- Chihuahua: Isotype. 46 km E of Tasajera, Sin., and 27 km E of La Paridia, Sin., on road to San Vicente, Chih., 1970 m. Near 26°46′N; 107°03′*W. M. Kimnach and H. Sánchez-Mejorada 2091 = HNT 39287 = U2528.*

Villadia minutiflora Rose ($n = 21$)
- Oaxaca: Ixtepec. *R. Moran and M. Kimnach 7768.*
- Oaxaca: 22 km from Mex 190 on road to Benito Juárez. *M. Kimnach, M. Cházaro, and M. Negrete 3222 = U3140.*

Villadia misera (Lindl.) R. T. Clausen ($n = 33, 42–44, 48–49$)
- San Luis Potosí Rocks E of road at summit 15 km N of Ahualulco. *C. H. Uhl 1541.* $n = 33$.
- Guanajuato: Below cliff 12 km W of Tierrablanca, 1770 m. *C. H. Uhl 1846.* $n = 33$.
- Querétaro: N slope Cerro del Mexicano, NW of Colón. *R. Moran 14763.*
- Querétaro: W of Esperanza. *R. Moran 10180.* $n = 33$.
- Querétaro: Km. 213.2, Cuesta China, 7 km E of Querétaro city, 1980 m. *C. H. Uhl 1488.* $n = 33$.
- Querétaro: Top of lava cliff, Mex 120, 5.5 km N of Quiotilla. *C. H. Uhl 2135.* $n = 33$.
- Hidalgo: Volcanic rock E side of Presa Madero, 12 km W of Huichapán. *C. H. Uhl 1475.* $n = 33$.
- Edo. México: Mex 57 at Km. 111.5, 10.5 km WNW of Soyaniquilpan. N. W. Uhl & W. Handlos. *U1483.* $n = 33$.
- Hidalgo: 1.5 km S of El Tepenene. *C. H. Uhl 1878.* $n = 33$.
- Hidalgo. Limestone ledges at Km. 64.5, 7.5 km SE of Tepeji del Río. N. W. Uhl and W. Handlos. *U1479.* $n = 33$.

TABLE 1. Continued.

Hidalgo: 2.5 km S of Epazoyucán. *R. Moran, H. Sánchez-Mejorada, and C. H. Uhl 13408. n* = 33.

Hidalgo: Volcanic rock, Km 19.3 on Mex 130 E of Pachuca. *C. H. Uhl 2346. n* = 33.

Edo. México: San Juan de Teotihuacán. *R. T. Clausen 47-42. n* = 33.

Puebla: Goat-scoured hillside W of Laguna de Alchichica. *C. H. Uhl 1886. n* = 33.

Cultivated: F. Schmoll, Cadereyta de Montes, Qro. *Clausen 46-12. n* = 33 (Fig. 14).

Querétaro: Limestone 7.4 km S of San Joaquín and 33 km E of Vizarrón, road to Maconi, 2250 m. *C. H. Uhl 2155. n* = 42.

Querétaro: Canyon at Km 60, 12 km N of Cadereyta, 4 km S of San Javier, 2200 m. *C. H. Uhl 2120. n* = 43.

Hidalgo: Near summit, W side of mountain SE of Santuario, 2590 m. *R. Moran and C. H. Uhl 13397. n* = 44 (Fig. 15).

Hidalgo: Gully 8 km N of Tepeji del Río. *C. H. Uhl 1473. n* = 42.

Cultivated: F. Schmoll, Cadereyta de Montes, Qro. *Clausen 47-13. n* = 44.

Aguascalientes: Sierra Fría. Granite (?) at Km 20.7, 5.5 km E of Tepezala, 2560 m. *C. H. Uhl 2108. n* = 48.

San Luis Potosí: Sierra de Alvarez, near Km 45 E of San Luis Potosí, 2300 m. *R. Moran 6326. n* = 49 (Fig. 17). *C. H. Uhl 1644* from nearby.

San Luis Potosí: 30 km S of Santa María del Río. *C. H. Uhl 1538B. n* = 48 (Fig. 16).

aff. *V. misera* (*n* = 9)

Coahuila: Oak woodland, S side of Sierra de la Viga, ca 8 km E of Jame, 48 km ESE of Saltillo, 2900 m. Near 25°21′N; 100°32′W. *J. Henrickson 16110B = U2462. n* = 9 (Fig. 12).

Villadia nelsonii Rose (*n* = 20).

Oaxaca: Sierra de Juárez. Km 221.8 on Mex 175, 18 km N of junction E of Oaxaca city, 2700 m. *C. H. Uhl 2372.*

Oaxaca: Sierra de San Felipe, 2000 m. *R. T. Clausen 6080.*

Oaxaca: Las Huertas, Cerro San Felipe. *R. Moran 10138.*

Oaxaca: Near Lachao, 1800 m. *R. Moran 10109* (Fig. 18).

Oaxaca: Km 182 on Oaxaca-Puerto Escondido road, 1825 m. *UC65-414.*

Oaxaca: Santo Domingo Ozolotepec, 2135 m. *T. Macdougall B-190 = UC58.828.*

Villadia painteri Rose (*n* = 15)

Zacatecas: Km 267 on Mex 54, ca 40 km SW of Zacatecas city. *J. and M. Bleck 216 = U1924* (Fig. 19).

Zacatecas: E of Mex 54 at Km 245.5, 10.5 km S of Villanueva, 1920 m. *C. H. Uhl 2258.*

Jalisco: Km 6 W of Ojuelos de Jalisco, 2320 m. *C. H. Uhl 2106.*

Jalisco: Volcanic cliff 36 km S of Ojuelos de Jalisco. *C. H. Uhl 2143.*

Guanajuato: Granite (?) near summit of Picachos de la Bufa, NE side of Guanajuato city, 2285 m. *C. H. Uhl 2113.*

Guanajuato: Cliff W of summit, Cerro Cubilete, W of Guanajuato city, 2530 m. *C. H. Uhl 2111.*

Villadia patula Moran and C. H. Uhl (*n* = 13)

San Luis Potosí: Type collection. 6 km SE of Zaragoza. Near 22°01′N; 100°43′W. *R. Moran and M. Kimnach 7655.*

San Luis Potosí: 1.5 km N of Santo Domingo. *R. Moran and M. Kimnach 7670* (Fig. 20).

Guanajuato: 7 km NW of San José Itúrbide, 2200 m. *R. Moran and M. Kimnach 7672.*

Querétaro: Road to Maconi, 7 km S of San Joaquín, 33 km E of Vizarrón, 2250 m. *C. H. Uhl 2133.*

Villadia pringlei Rose (*n* = 16)

Durango: 18 km W of Tepehuanes toward Topía, 2250 m. *M. Kimnach and F. K. Brandt 1184 = HNT 21328 = U2053* (Fig. 21).

TABLE 1. Continued.

Villadia recurva Moran, Kimnach, and C. H. Uhl (*n* = 14)

Guerrero: Km 10.2 E of Chilpancingo toward Tixtla. *C. H. Uhl 1441.*

Oaxaca: Before San Pedro Yosoñama from Tlaxiaco, 2200 m. *M. Kimnach 3320 = U3141.*

Oaxaca: Type collection. Lachao. *R. Moran 10107* (Fig. 23).

Villadia sp. aff. *recurva* (*n* = 12)

Oaxaca: Near Tlaxiaco?. *R. T. Clausen 53-21* (Fig. 24).

Villadia squamulosa (S. Watson) Rose (*n* = 17)

Texas: Big Bend National Park. N side of Casa Grande, E of Panther Pass, 1850 m. *C. H. Uhl 1673.*

Texas: Big Bend National Park. Boot Canyon, above Boot Springs cabin. *C. H. Uhl 874* (Fig. 22).

Sedum (formerly in *Altamiranoa* Rose)

Sedum andinum Ball (*n* = 40–48, irregular)

Peru: Dept. Lima, Prov. Huarochiri. Río Rímac, canyon of Río Blanco, 3500 m. *P. C. Hutchison 591 = UC 52.623*

Peru: Probably from same locality. *P. C. Hutchison 621 = UC 52.727.*

Peru: Dept. Tacna, Prov. Tarata. 17 km NE of Quilla and ca 62 km NE of Tacna toward Tarata, 3100 m. *P. C. Hutchison and J. K. Wright 7183 = UC 64.1502* (Fig. 26).

Sedum goldmanii (Rose) Moran (n = 25)

Michoacán: Lava 3.5 km S of Paracho and 31 km N of Uruapan, 2250 m. *C. H. Uhl 1401.*

Michoacán: Fir forest, 24 km S of Pátzcuaro. E. P. Edwards. *R. T. Clausen 48-40.*

Edo. México: San Ignacio. *R. Moran and M. Kimnach 7678.*

Edo. México: 5 km S of Temascalcingo. *M. Kimnach 490 = HNT 16780 = U1293.*

Edo. México: Rocks above San Mateo Oztotitlán, SW side of Cerro Teresona, just N of Toluca, 2750 m. *C. H. Uhl 1421.*

Edo. México: Igneous rock, Km 33.5 on Mex 134 SW of Toluca, 3020 m. *C. H. Uhl 2513.*

Edo. México: Nevado de Toluca, 4 km ESE of San Juan. *R. T. Clausen 6020.*

Edo. México: Above Lerma. Near topotype of *Altamiranoa ramulosa* Fröd. *R. Moran and M. Kimnach 7690.*

Edo. México: La Carbonera. *R. Moran and M. Kimnach 7700.*

Edo. México: Zempoala. Topotype of *Cotyledon batesii* Hemsl. *R. Moran 10166.*

Edo. México: Sierra de las Cruces. *R. T. Clausen TMV-SLC.*

Hidalgo: Encarnación. H. Fittkau. *M14784.*

Hidalgo: 7.5 km SE of Tepeji del Río, Km 64.5 on Mex 57. N. W. Uhl and W. Handlos. *U1480.*

Hidalgo: Near topotype of *Umbilicus mexicanus* Schltdl. Above road to Mineral del Chico. *C. H. Uhl 1467.*

Hidalgo: San Miguel Regla. *R. Moran and M. Kimnach 7787.*

Hidalgo: Limestone N of Mex 130 at Km 119.6, 21 km W of Tulancingo. *C. H. Uhl 1559.*

Hidalgo: Peñas del Cuervo. *R. Moran 10079.*

Distrito Federal: Lava S of Mexico City, 2440 m. 19°19′N; 99°12′W. *R. T. Clausen and J. L. Edwards 7440.*

Distrito Federal: Lava, 2 km S of Desierto de los Leones, Sierra de las Cruces. 19°17′N; 99°19′S. *R. T. Clausen 7522* (Fig. 31).

Distrito Federal: Lava SW of Topilejo, 2850 m. Near 19°10′N; 99°03′W. *R. Moran 6403.*

Tlaxcala: NW of Mount Malinche. *R. T. Clausen TMV MR3.*

Tlaxcala: Manantiales de la Concha, Mt. Malinche, 3780 m. *E. K. Balls 5650 = R. T. Clausen 5701c.* Probably triploid.

Puebla: Cerro Oriental, near Oriental, *E. J. Alexander 1834 = U209.*

Puebla: NE of summit 13 km NE of Acatzingo. *C. H. Uhl 1552.*

Puebla: Km 9, Mex 144, near Esperanza, 2590 m. *C. H. Uhl 2360.*

TABLE 1. Continued.

Sedum grandisepalum R. T. Clausen ($n = 44$)
- Oaxaca: Type collection. Santo Tomás Teipan, San Carlos Yautepec, 2135 m. 16°20′N; 95°35′W. *T. MacDougall B-102 = Clausen 48-35* (Fig. 27).

?*Sedum* ?*grandyi* Raym.-Hamet ($n = 38$–40)
- Cultivated: J. Marnier-Lapostolle, ''Les Cedres'', St. Jean Cap Ferrat, France. *U1754* (Fig. 28)

Sedum jurgensenii (Hemsl.) Moran ssp. *jurgensenii* ($n = 23$)
- San Luis Potosí: Mex 120 from Xilitla past Ahuacatlán, 1765 m. *F. Boutin 3437 = HNT 28862 = U2317.*
- Guanajuato: Radamaderos. *A. Lau 079 = HNT 41310 = U2582.*
- Querétaro: Limestone at summit at Km 228.7, 26 km SW of Xilitla, SLP, 1700 m. *C. H. Uhl 1860.*
- Querétaro: Limestone 1 km S of San Joaquín, 37 km NE of Vizarrón, 2360 m. *C. H. Uhl 2130.*
- Hidalgo: Cantil de Tambor, 11 km S of Santa Ana, 35 km N of Jacala, 1650 m. *C. H. Uhl 1866.*
- Hidalgo: Barranca de Mármoles, Km 64, 26 km N of N road to Zimapán. *C. H. Uhl U2345.*
- Hidalgo: S of Zacualtipán. *R. Moran 10064.*
- Hidalgo: Topotype of *Altamiranoa elongata* Rose. Above Pachuca. *R. Moran and M. Kimnach 7782* (Fig. 29).
- Hidalgo: l km NE of Pachuca city limit. *C. H. Uhl 1471.*
- Puebla: Topotype of *Altamiranoa necaxana* Fröd. Km 204.4, 11 km E of Huauchinango and 0.4 km E of dam and spur road to Nuevo Necaxa. *C. H. Uhl 1555* (Fig. 30).
- Puebla: 4.2 km E of Aquixtla on road to Tetela de Ocampo. *C. H. Uhl 2356.*
- Puebla: Volcanic rock below waterfall, 3 km S of Zacatlán, 2135 m. *C. H. Uhl 2350.*
- Veracruz: Canyon of Gemapa River, 5 km N of Coscomatepec. *R. T. Clausen TMV-O-G2.*
- Cultivated: *R. Moran 3300, UC46-778.*
- Cultivated: F. Schmoll, Cadereyta de Montes, Qro. *R. T. Clausen 46-17, 47-9, 47-63,* and *47-74.*

Sedum jurgensenii ssp. *attenuata* Moran ($n = 23$)
- Puebla: Type collection. Limestone canyon NE San Hipólito. *R. Moran and M. Kimnach 7776.*
- Puebla: Inside crater with lake at Atenco, 2500 m. *C. H. Uhl 2364.*
- Puebla: Lava 10 km S of Ciudad Serdán, 2560 m. *C. H. Uhl 1897.*

Sedum latifilamentum R. T. Clausen ($n = 20$)
- Querétaro: S of summit at Km 131.2, 5 km N of Maguey Verde, 8 km S of Pinal de Amoles, 2590 m. *C. H. Uhl 1855.*
- Hidalgo: Type collection. Low sandstone cliffs in pine/oak forest, Mount Cangando, 2 km E of Encarnación, 2490 m. *R. T. Clausen C78-15* (Fig. 34).

Sedum scopulinum (Rose) Moran ($n = 28$)
- Puebla: Lime hills N of Tehuacán. H. E. Moore Jr. *U839.*

Sedum sp. ($n = 20$)
- Oaxaca: Cerro San Felipe. *R. Moran 10135.*
- Cultivated: Cerro San Felipe, Oaxaca. Collected by T. MacDougall *= Moran 12008 = U1666* (Fig. 32).
- Oaxaca: 3 km SW of Portillo San Andrés. *R. Moran and M. Kimnach 7757.* $n = 20$.

Sedum sp. ($n = 29$)
- Jalisco: La Joya, N. slope of Nevado de Colima, 3320 m. *F. C. Boutin and F. K. Brandt 2310 = HNT 23573 = U2059* (Fig. 33).

Sedum sp. ($n =$ ca. 50, irreg.)
- Peru: Dept. Piura, Prov. Huancabamba. 7 km above Huancabamba toward Canchaque, 2450 m. *P. C. Hutchison and J. K. Wright 6621 = UC 64.861*

er cells. The photographs are from marked cells on permanent slides, mostly using phase optics. Voucher specimens are in the Bailey Hortorium of Cornell University.

SPECIES AND OBSERVATIONS

Below and in Table 1, having as yet no satisfactory classification, we list the species alphabetically, first those of *Villadia,* then those of *Sedum* formerly placed in *Altamiranoa.* In most species all collections have the same chromosome number, and we list them roughly from north to south and from west to east. Chromosomes of all species are very small, and except as noted we cannot differentiate any of them by their appearance at metaphase I.

Villadia acuta Moran and C. H. Uhl (1991b) is herbaceous, with close-set, spreading, sharply acute leaves and a spike of white flowers, the corolla with a long tube and very acute, spreading lobes. It is known only from the type locality in south-central San Luis Potosí. It has 16 pairs of chromosomes (Fig. 1), as does the related *V. pringlei* of Chihuahua and Durango.

Villadia albiflora (Hemsl.) Rose (including *V. ramosissima* Rose) is a twiggy tangle, with spreading arrowhead leaves and open spikes of inconspicuous flowers with erect white corolla segments. It is rather common in southeastern Puebla and adjacent northern Oaxaca. Eleven collections, including a topotype of *V. ramosissima,* all had 15 pairs of chromosomes (Fig. 2), a number found also in *V. aperta* and *V. painteri,* both quite different in appearance. A hybrid between *V. albiflora* (*U1455*) and *V. recurva* (*U1441,* $n = 14$) had only 4–8 paired chromosomal elements at metaphase I, with many unpaired; and disjunction at anaphase I was unbalanced, since metaphase II plates showed 12–15 chromosomes. A hybrid with *V. nelsonii* (*Moran 10109,* $n = 20$) formed 13–14 paired elements and 2–4 unpaired at metaphase I (14 + 2 in Fig. 35). One with *Sedum alamosanum* S. Watson (*U1647,* $n = 18$) showed only a little chromosome pairing at meiosis.

Villadia aperta Moran and C. H. Uhl (1992) is a small herb with an open thyrse of pale greenish-yellow flowers having bowl-shaped corollas. It is known from only one plant from a cliff on the western brink of the Sierra Madre Occidental of Durango, near the Sinaloa border. It has 15 pairs of chromosomes (Fig. 3), as do *V. albiflora* and *V. painteri,* neither of which seems closely related. A hybrid between *V. aperta,* as pollen parent, and *Sedum greggii* Hemsl. ($n = 33$) had 20 or more unpaired chromosomes at metaphase I of meiosis (Fig. 36); the 15 chromosomes from the *Villadia* parent are noticeably larger than the small *Sedum* chromosomes.

Villadia aristata Moran (1990) has simple stems with close-set ascending leaves and a dense thyrse of white or pinkish flowers, the corolla ellipsoid, with segments rounded and denticulate at the tip and with a conspicuous dorsal spur. It grows in the Sierra Madre Oriental from southeastern Coahuila and southern Nuevo León and Tamaulipas for nearly 250 km south-southwest to the Sierra de Alvarez, east of the city of San Luis Potosí. Seven collections each had ten pairs of chromosomes (Fig. 4), as found also in a very different collection from Querétaro somewhat resembling *V. cucullata.*

Villadia cucullata Rose of northeastern Mexico has tall often solitary stems with crowded ascending leaves and with a conspicuous dense spike of red to orange-yellow flowers, the corolla ellipsoid, nearly closed, its segments denticulate. In subsp. *cucullata* (including *V. jimulcensis* Nesom), which grows mostly within about 75 km of Saltillo in southeastern Coahuila, the corolla segments are rounded and cucullate. Our five collections all had $n = 11$ (Fig. 5), a number unique to this species.

V. cucullata subsp. *apiculata* Moran and C. H. Uhl (1998) differs in its strongly keeled corolla segments, narrowed at the apex, and each with a subdorsal spur. It ranges from southwestern Tamaulipas south to northern Hidalgo. A plant of the type collection from San Luis Potosí and another from Hidalgo both also had $n = 11$ (Fig. 6). In a plant from Tamaulipas, however, most cells at metaphase I (Fig. 25) had 21 pairs, plus an unpaired chromosome of standard size. Apparently it is a tetraploid that lacks a chromosome ($4n - 1$).

Villadia sp. aff. *cucullata* has tuberous roots and is generally similar to *V. cucullata* but differs in its brownish corolla and in its chromosome number. It has $n = 10$ (Fig. 7), as in the white-flowered *V. aristata.* We know it from a single plant from northwestern Querétaro, and we need more information.

Villadia guatemalensis Rose (including *V. levis* Rose) is a coarse plant, sometimes bushy, with minutely papillate stems and spreading acute leaves, the corolla greenish-yellow to white and often strongly flecked with red, with spreading segments. Nine collections from northern and central Oaxaca and two from southern Guatemala all had $n = 21$ (Fig. 8). However, two collections from southeast of Oaxaca city had $n = 20$, with one pair noticeably larger than the others and perhaps corresponding to two pairs in the other collections (Fig. 9). One other collection was meiotically irregular and probably triploid. In a hybrid between the 20-chromosome race and *V. nelsonii* (also $n = 20$) metaphase I had 15–20 paired elements and 0–8 unpaired (approximately 15 + 8 in Fig. 37). Hybrids of the same collection of *V. guatemalensis* with the 26-chromosome race of *Sedum greggii* (*Moran 14730*) and with the tetraploid *S.* (*Villadia*) *grandisepalum* ($n = 44$) had many unpaired chromosomes at meiosis (Uhl, 1994).

Villadia imbricata Rose is a distinctive low herb with crowded mammillate leaves and a short spike or raceme of small white flowers, the corolla elliptic, of thick segments. Five collections from southern Puebla and northeastern Oaxaca had $n = 12$ (Fig. 10), as did two from cultivation, one of them with two small extra B-chromosomes (Fig. 11).

Villadia incarum (Ball) Baehni and J. F. Macbr. is a little-known Peruvian species, with terete leaves and a short raceme of yellowish or reddish flowers. We had three collections under this name. At metaphase I $n = 88–89$, with chromosomes that are variable in size and relatively large for *Villadia* (Fig. 13).

Villadia laxa Moran and C. H. Uhl (1995) is a slender herb with papillose-roughened stems and with a raceme or lax thyrse of rosy flowers, the corolla with spreading segments. It is the northwesternmost *Villadia,* native to the Sierra Madre Occidental of northern Sinaloa and adjacent southern Sonora and southwestern Chihuahua. A plant of the type collection had $n = 14$, a number found also in the very different *V. recurva* of Guerrero and Oaxaca.

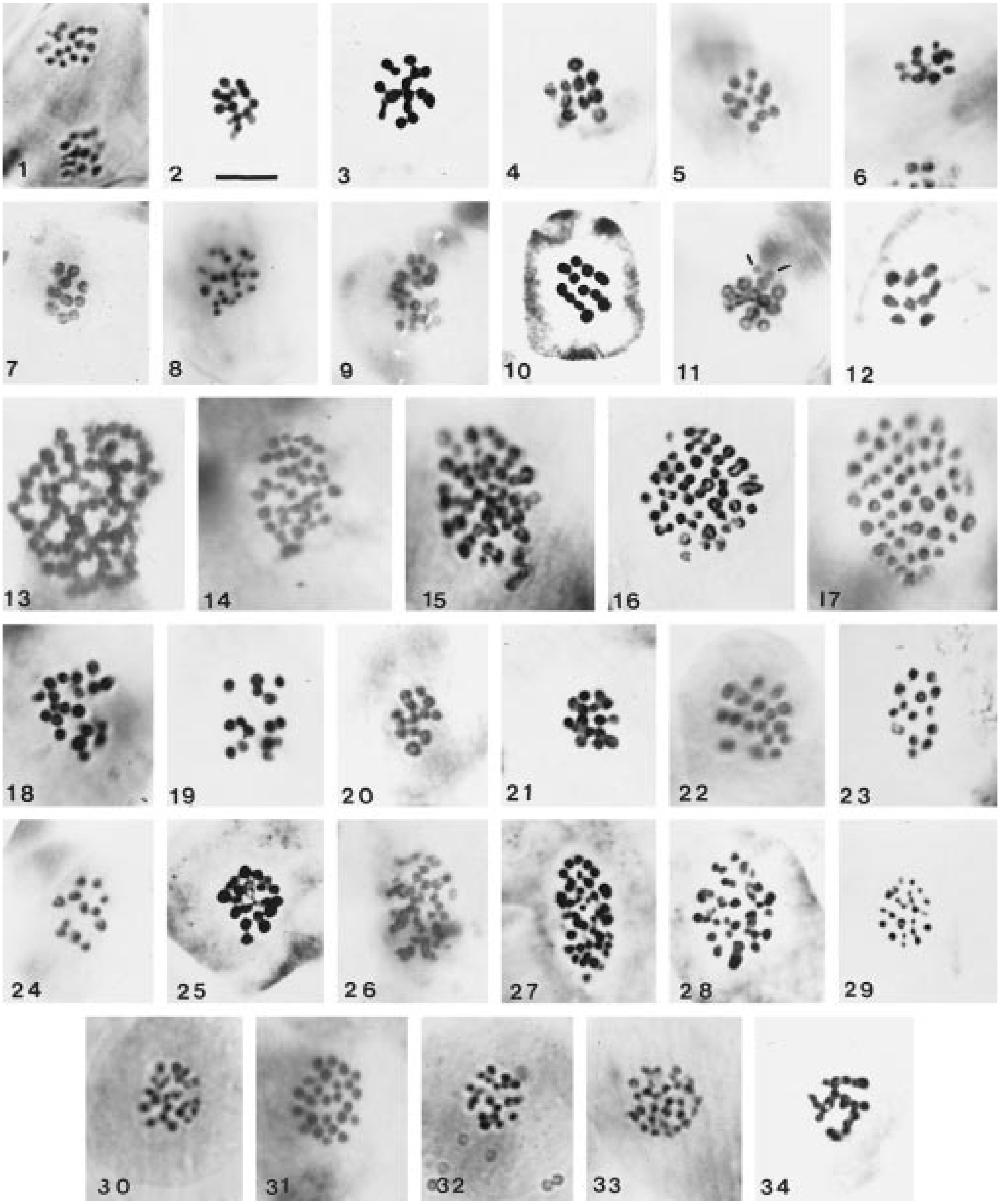
Villadia minutiflora Rose is a slender herb with papillose stems and bristly-ciliate leaves and sepals, the corolla small, white or flushed with red, with spreading segments. It is known only from the Sierra de Juárez just north of the city of Oaxaca. Plants from two localities had $n = 21$, a number found also in the very different *V. guatemalensis.*

Villadia misera (Lindl.) R. T. Clausen (= *V. parviflora* Rose) has tuberous roots and short, simple stems that die to the ground after flowering, with many ascending leaves and a narrow thyrse of small and inconspicuous flowers, the corolla white, with erect segments. It is widespread in eastern Mexico, typically in barren places. From western San Luis Potosí southeastward for 330 km across the altiplano and the dry western side of the Sierra Nevada Oriental to the west side of the Cofre de Perote volcano in Puebla, 14 collections had $n = 33$ (as also one other from cultivation), with chromosomes mostly about the same size (Fig. 14). Five more collections from Querétaro and adjoining Hidalgo had $n = 42–44$ (Fig. 15) and four others from scattered northern localities in San Luis Potosí and Aguascalientes had $n = 48–49$ (Figs. 16, 17), all with chromosomes differing substantially among themselves in size. These numbers in *V. misera* may represent tetraploids and hexaploids of some sort, derived from a common ancestor with the rather similar *V. painteri,* a diploid with $n = 15$ (Fig. 19), which grows just to the northwest. However, we have no hybrids of *V. painteri* or *V. misera* that might shed light on polyploidy here. Further study might support separating these chromosome races taxonomically.

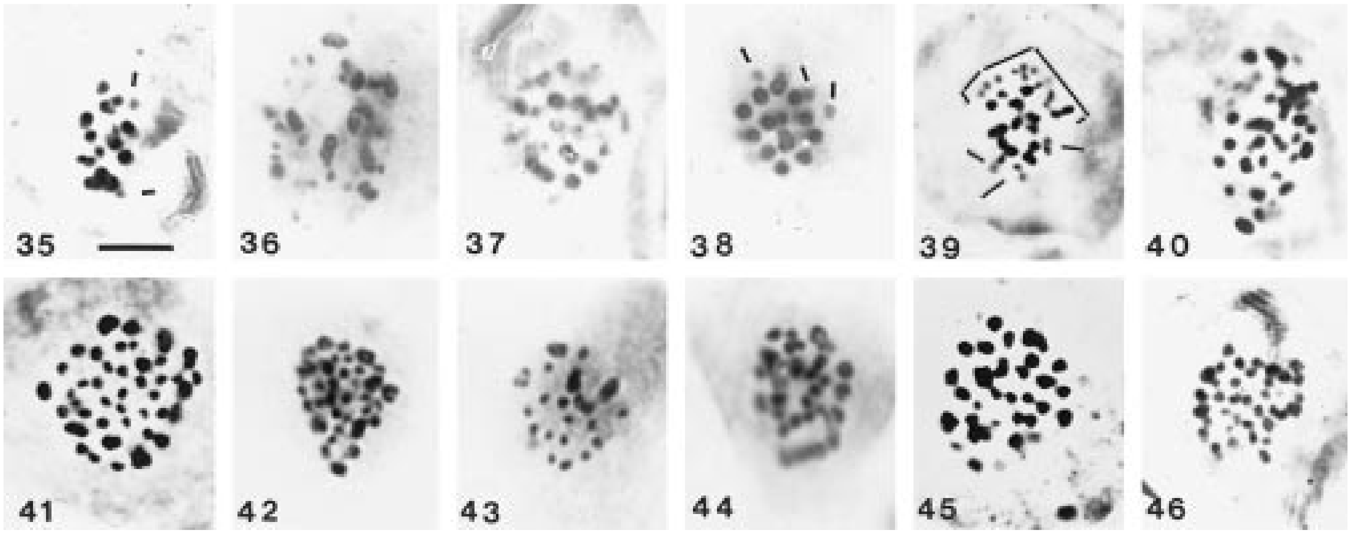
V. sp. aff. *misera* is known to us from a single collection from extreme southeastern Coahuila. It is rather similar to *V. misera,* but it came from farther north, and it had far fewer chromosomes, $n = 9$, the lowest number found in the genus (Fig. 12).

Villadia nelsonii Rose is bushy and papillose, with scattered, broad, uniquely spatulate leaves and with a spike or spicate thyrse of white flowers, the corolla segments spreading (Moran, 1970). Six collections from central and southern Oaxaca all had $n = 20$ (Fig. 18). Hybrids with *V. albiflora* ($n = 15$) and *V. guatemalensis* ($n = 20$) are mentioned above. A hybrid with *V. recurva* (*U1441,* $n = 14$) formed 12–14 paired elements and 0–8 unpaired at metaphase I (13 + 3 in Fig. 38). One with a topotype of *Altamiranoa necaxana* Fröd., which we consider merely a near-glabrous form of the mostly puberulent *Sedum jurgensenii* (*U1555,* $n = 23$), had 17–19 paired elements and 2–7 unpaired. Intergeneric hybrids of *V. nelsonii* with *Cremnophila nutans* (Rose) Rose ($n = 33$) (ca. 13 paired + 18 unpaired elements in Fig. 39), with *Pachyphytum hookeri* (Salm-Dyck) A. Berger ($n = 32$) (ca. 16 + 19 in Fig. 40), with *Sedum craigii* R. T. Clausen ($n = 30$) and with *S. palmeri* S. Watson ($n = 34$) all showed less chromosome pairing (Uhl, 1994).

V. painteri Rose is rather similar to *V. misera,* but the corolla is slightly smaller and has obtuse segments. We refer our plants here tentatively because we have had no live material from the type locality (Barranca de Guadalajara) for comparison. We had six collections, slanting



Figs. 1–34. Chromosomes of *Villadia* and *Sedum* (formerly *Altamiranoa*) species at metaphase I of meiosis, except as indicated, all ×2000. **1.** *V. acuta, U1278, n* = 16 (metaphase II). **2.** *V. albiflora, C51–15, n* = 15. **3.** *V. aperta, U2255, n* = 15. **4.** *V. aristata, Moran 10006, n* = 10. **5.** *V. cucullata, UC52.361, n* = 11. **6.** *V. cucullata* ssp. *apiculata, U834, n* = 11. **7.** *V.* sp. aff. *cucullata, U2122, n* = 10 (metaphase II). **8.** *V. guatemalensis, U2055, n* = 21. **9.** *V. guatemalensis, Moran and Kimnach 7752, n* = 20. **10.** *V. imbricata, U2368, n* = 12. **11.** *V. imbricata, U708,n*



Figs. 35–46. Chromosomes of *Villadia* and *Sedum* (formerly in *Altamiranoa*) hybrids at metaphase I of meiosis, except as indicated, all ×2000. Lines in some figures indicate unpaired chromosomes. Seed parent listed first. **35.** *V. nelsonii* (*Moran 10109, n* = 20) × *V. albiflora* (*U1455, n* = 15); 14 paired elements + 2 univalents. **36.** *Sedum greggii* (*Moran and Kimnach 7807, n* = 33) × *V. aperta* (*U2255, n* = 15); mostly unpaired, with larger elements from the *Villadia* parent. **37.** *V. nelsonii* (*Moran 10109, n* = 20) × *V. guatemalensis* (*Moran and Kimnach 7752, n* = 20); ca. 15 paired + 8 unpaired elements. **38.** *V. nelsonii* (*Moran 10109, n* = 20) × *V. recurva* (*U1441, n* = 14); 13 paired elements + 3 univalents (lines). **39.** *Cremnophila nutans* (*Moran 10174, n* = 33) × *V. nelsonii* (*Moran 10109, n* = 20); 13 paired + 18 unpaired elements. **40.** *Pachyphytum hookeri* (*Moran 13349, n* = 32) × *V. nelsonii* (*Moran 10109, n* = 20); ca. 16 paired + 19 unpaired elements, the larger from *Villadia*. **41.** *Graptopetalum fruticosum* (*U1078, n* = 31) × *V. recurva* (*U1441, n* = 14); 43 elements, nearly all univalents, with 14 larger from the *Villadia* parent. **42.** *Pachyphytum hookeri* (*Moran 13349, n* = 32) × *V. recurva* (*Moran 10107, n* = 14); 36 elements, with 14 larger from the *Villadia* parent. **43.** Same hybrid. Metaphase II with four large chromosomes from *Villadia,* 18 smaller from *Pachyphytum*. **44.** *Sedum greggii* (*U1491, n* = 33) × *V. recurva* (*Moran 10107, n* = 14); ca. 30 elements. **45.** *S. grandisepalum* (*Clausen 48–35, n* = 44) × *S. alamosanum* (*U1647, n* = 18); ca. 22 paired + 12 unpaired elements. **46.** *Sedum alamosanum* (*U1647, n* = 18) × *S. latifilamentum* (*U1855, n* = 20); 38 unpaired elements. Bar = 5 μm.

250 km southeastward across the dry altiplano from south-central Zacatecas, through the northeastern tip of Jalisco, to Guanajuato city. All had n = 15 (Fig. 19), as in the very different *V. albiflora* and *V. aperta. Villadia misera,* with n = 33, 42–44, and 48–49, may have evolved from tetraploids and hexaploids related to *V. painteri.*

Villadia patula Moran and C. H. Uhl (1991a) has somewhat the habit of *V. misera,* with many ascending leaves and a slender thyrse. However, the flowers are larger, with an open corolla and with long slender styles; and the plant seems closer to *V. guatemalensis.* We studied four collections from mountains along the east side of the central altiplano, from the type locality in southwestern San Luis Potosí, for nearly 200 km southeastward across eastern Guanajuato, to northeastern Querétaro. All had n = 13 (Fig. 20), a number unique to this species.

Villadia pringlei Rose, from the Sierra Madre Occidental in Chihuahua and Durango, has a dense spike or thyrse, the corolla white with segments strongly outcurved at the tips. It somewhat resembles *V. acuta* of southern San Luis Potosí 600 km to the southeast but is smaller and has a more branched inflorescence. A single collection from northwestern Durango had n = 16 (Fig. 21), as in *V. acuta.*

Villadia recurva Moran, Kimnach, and C. H. Uhl (1998) is erect or somewhat decumbent and branching, the corolla white or purplish red, campanulate with widely recurving segments. It grows in the Sierra Madre del Sur of eastern Guerrero and western Oaxaca. Three collections had n = 14 (Fig. 23), a number found also in the very different *V. laxa* of northwestern Mexico. Hybrids of *V. recurva* with *V. albiflora* (n = 15) and with *V. nelsonii* (n = 20) are cited above, and a hybrid with the tetraploid *Sedum* (once *Villadia*) *grandisepalum* R. T. Clausen (n = 44) is mentioned below. Intergeneric hybrids with *Graptopetalum fruticosum* Moran (n = 31) (ca. 43 elements in Fig. 41), with *Pachyphytum hookeri* (n = 32) (ca. 36 elements at metaphase I in Fig. 42, 22 elements at metaphase II in Fig. 43), and with *Sedum greggii* (n = 33) (30 elements in Fig. 44), were all highly

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←

= 12 + 2B (lines). **12.** *V.* sp. aff. *misera, U2462, n* = 9 (anaphase I). **13.** *V. incarum, C42–32, n* = 88. **14.** *V. misera, C46–12, n* = 33. **15.** *V. misera, Moran 13397, n* = 44. **16.** *V. misera, U1538B, n* = 48. **17.** *V. misera, Moran 6326, n* = 49. **18.** *V. nelsonii, Moran 10109, n* = 20. **19.** *V. painteri, U1924, n* = 15. **20.** *V. patula, Moran and Kimnach 7670, n* = 13. **21.** *V. pringlei, U2053, n* = 16. **22.** *V. squamulosa, U874, n* = 17. **23.** *V. recurva, Moran 10107, n* = 14. **24.** *V.* sp. aff. *recurva, C53–21, n* = 12. **25.** *V. cucullata* ssp. *apiculata, U2076, n* = 21 + 1. **26.** *Sedum* cf. *andinum, UC64.1502, n* = ca. 40. **27.** *S. grandisepalum, C48–35, n* = 44. **28.** *S. grandyi, U1754, n* = ca. 40. **29.** *S. jurgensenii, Moran and Kimnach 7782, n* = 23. **30.** *S jurgensenii* (*V. necaxana*)*, U1555, n* = 23. **31.** *S. goldmanii, Clausen 7522, n* = 25. **32.** *S.* sp., *U1666, n* = 20. **33.** *S.* sp. *U2059, n* = 29. **34.** *S. latifilamentum, Clausen 78–15, n* = 20. Bar = 5 μm.

irregular at meiosis (Uhl, 1994). In all these hybrids the *Villadia* chromosomes were distinguishable by their larger size.

Villadia sp. aff. *recurva.* In 1953 R. T. Clausen grew a plant from the Sierra Madre del Sur of northwestern Oaxaca, of which we found a good photograph but no specimen and no precise locality or source. We agree with him that it looks like a new species. It has $n = 12$ (Fig. 24), as in the rather different *V. imbricata,* but it more resembles *V. recurva,* which has $n = 14$.

Villadia squamulosa (S. Watson) Rose is a slender herb with an open spike or narrow thyrse of small rose-colored flowers, the corolla with spreading segments, and with relatively large flabellate nectaries. It is the northernmost species, growing in the mountains of Chihuahua, Durango, Zacatecas, and the Big Bend region of western Texas, where it is the only species native to the United States. Two collections from Big Bend National Park had $n = 17$ (Fig. 22), a number apparently unique in *Villadia.*

Sedum species formerly in Altamiranoa—*Sedum andinum* Ball is a small tufted Peruvian plant with minute hemispheric leaves and a small cyme of red flowers. Two collections supposedly from near the type locality, east of Lima, had many unpaired chromosomes at metaphase I and a somatic number estimated at very close to 100. It is not clear whether the meiotic irregularity was due to a hybrid origin or to odd-ploidy. A plant, possibly a different species, from more than 800 km to the southeast in far southern Peru about 30 km from the border with Chile, was nearly normal at meiosis except for several large elements at metaphase I. Allowing for these presumed multivalents, $n = 40$ probably (Fig. 26).

Sedum goldmanii (Rose) Moran is a common plant in the mountains of central Mexico, generally on old lava. It is best known as *Villadia batesii* (Hemsl.) Baehni and J. F. Macbr., but it is highly variable and also includes *Altamiranoa alpina* Fröd., *A. batesii* var. *subalpina* Fröd., *A. ramulosa* Fröd., and *V. mexicana* (Schltdl.) H. Jacobsen (Moran, 1997b). The plant is often much branched from the base and bears a cyme of white or reddish flowers that are unique in having the corolla tube equaling the lobes. We studied 26 collections from throughout the range, from western Michoacán across the state of México, southern Hidalgo, the Federal District and Tlaxcala to southeastern Puebla, including near topotypes of *A. ramulosa* Fröd., *Cotyledon batesii* Hemsl., and *Umbilicus mexicanus* Schltdl. Though one collection was meiotically irregular and probably triploid, the other 24 all had $n = 25$, a number so far found only in this species.

Sedum grandisepalum R. T. Clausen has small cymes with greenish-yellow petals that are generally shorter than the sepals. After originally describing it in *Sedum,* Clausen (1959) later transferred it to *Villadia;* we now believe it is best kept in *Sedum* with the other Altamiranoas. It is known only from the type collection, from the eastern Sierra Madre del Sur of southern Oaxaca. It has $n = 44$ (Fig. 27), but meiosis is slightly irregular, with occasional univalents and probable multivalents.

Uhl (1994) crossed *Sedum grandisepalum* ($n = 44$) with four species considered to be diploids: *Villadia recurva* ($n = 14$), *V. guatemalensis* ($n = 20$), *Sedum alamosanum* ($n = 18$) (ca. 22 paired + 12 unpaired elements in Fig. 45), and *S. obcordatum* R. T. Clausen ($n = 34$). As expected in triploid hybrids, each hybrid looked more like *S. grandisepalum* than like the other parent. Also, each hybrid formed 17–22 paired elements (bivalents and multivalents) at meiosis, with a large number of unpaired chromosomes. We conclude that *S. grandisepalum* is tetraploid with a basic number of $x = 22$ and that its 44 chromosomes formed the paired elements in these hybrids. The chromosomes from the diploid parents had no full homologues, and except for a few that occasionally attached to corresponding parts of a *grandisepalum* chromosome, most remained unpaired.

Supporting this conclusion, when *S. grandisepalum* ($n = 44$) was crossed with another tetraploid, *Echeveria chapalensis* Moran and C. H. Uhl ($n = 45$), the hybrid was more intermediate in appearance, and at meiosis it formed 33–40 paired and 2–7 unpaired elements. Here again, we believe that most or all the paired elements were of homologous chromosomes of the two sets from the same tetraploid parent. However, the presence of multivalents suggests some pairing between chromosomes of the different parents, and univalents hint that some homologies between corresponding chromosomes from the same parent may be weak. In their chromosome pairing the parents seem not to be typical autotetraploids.

Sedum grandyi Raym.-Hamet of northern Peru has short stems, broadly ovate to suborbicular leaves ca. 5 mm long, and a lax cyme of small flowers with corolla shorter than the calyx. A collection from cultivation, supposedly of this species, generally had a few univalents and multivalents at meiosis, suggesting hybridity or polyploidy; allowing for these, the gametic number is probably 38 (Fig. 28).

Sedum jurgensenii (Hemsl.) Moran, with weak elongate stems and with cymes of white flowers, is distinguished by its puberulent herbage. It has long been known as *Villadia elongata* (Rose) R. T. Clausen (Moran, 1997a). Primarily a plant of the wetter eastern slope of the Sierra Madre Oriental, it occurs from Guanajuato and southeastern San Luis Potosí south through northeastern Querétaro and Hidalgo to northern and eastern Puebla, edging into adjoining Veracruz. We studied plants of the typical subspecies from 13 localities throughout the range, including a topotype of *V. elongata,* and six others from cultivation. All had $n = 23$ (Fig. 29), a number known only in this species. *V. necaxana* (Fröd.) H. Jacobsen appears to be just a less puberulent form, and a plant from its type locality also had $n = 23$ (Fig. 30). Its hybrid with *V. nelsonii* ($n = 20$) is mentioned above. Subspecies *attenuata* Moran (1997a) differs in its strongly ascending and imbricated, narrower, and more sharply acute leaves. The type collection and two others also had $n = 23$.

Sedum latifilamentum R. T. Clausen, though never formally assigned to *Altamiranoa,* clearly belongs with that group, whatever its status. It has tuberous roots and white, globular corollas. The incurved petal tips, separating 2 mm or less at anthesis, the stamens, and the sulcate carpels without styles suggest that it is self-pollinated. We studied the type collection, from northern Hidalgo, and another plant, from northeastern Querétaro. Both had $n = 20$ (Fig. 34), a number found also in *Villadia guatemalensis* and *V. nelsonii* and in an unnamed plant from Oaxaca. A hybrid with *Sedum alamosanum* (*n* = 18) had little or no chromosome pairing at meiosis (38 univalents in Fig. 46), and one with *Graptopetalum fruticosum* (*n* = 31) appeared authentic but never flowered in 10 yr (Uhl, 1994).

Sedum scopulinum (Rose) Moran is a rare plant of southern Puebla, whose creeping stem bears persistent enlarged white leaf bases and a small cyme of white flowers. A single plant had *n* = 28.

Sedum sp. of central Oaxaca has obtuse leaves, and the pistils are oblong and rather broad, narrowing abruptly to the slender styles. Three collections had *n* = 20 (Fig. 32), as in *S. latifilamentum* of Hidalgo and Querétaro.

Sedum sp. from high on the Nevado de Colima in western Mexico somewhat resembles *S. goldmanii* but differs in its much shorter corolla tube and in other ways, and it has *n* = 29 (Fig. 33), a number known only from this collection.

Sedum sp. An unidentified collection from extreme northern Peru, like most of our other collections from South America, was irregular at meiosis. It had about 50 elements at metaphase I and many chromosome bridges and laggards at anaphase I; it appears to be a hybrid.

DISCUSSION

Villadia (sensu stricto) is extremely dysploid. We have found every gametic chromosome number from 9 to 17, as well as 20, 21, and scattered higher numbers to 89. These diverse numbers have been helpful in sorting out the species. As in *Echeveria* (Uhl, 1992) and Mexican *Sedum* (Uhl, 1985) diploid and tetraploid numbers intergrade or overlap, with no sharp boundary.

DNA studies are needed to show whether *Villadia* is monophyletic or whether some species may have evolved independently from different *Sedum* ancestors. We consider more primitive such species as *V. nelsonii* (*n* = 20) and *V. guatemalensis* (*n* = 20, 21), which are more branched and often woody at the base, with thyrsoid inflorescences, larger flowers, short corolla tubes and spreading segments, and long styles; and we note that these species generally have more but smaller chromosomes. On the other hand, we take as more specialized such species as *V. aristata* (*n* = 10) and *V. cucullata* (*n* = 11), which are less branched and often die to the base after flowering, with narrower, more spicate inflorescences, smaller flowers, longer corolla tubes and more erect segments and short and abruptly out-turned styles. These species generally have fewer but larger chromosomes. At meiosis in diploid intergeneric hybrids the chromosomes of the *Villadia* parent can often be distinguished by their larger size from those of the other parent (Figs. 39–43).

As with *Villadia*, apparently so also with species of *Sedum* formerly in *Altamiranoa*: our few hybrids with diploid species again seem to show that the species with low numbers (*n* = 20, 23) are effectively diploid. However, *Sedum grandisepalum* (*n* = 44) is tetraploid, and in all its hybrids most of the corresponding chromosomes of its two sets apparently pair preferentially with each other.

Hybrids of *Villadia* with diploid species generally have multivalents at meiosis, showing that parts of a chromosome from one parent are homologous with parts of two or more chromosomes from the other. Also, most hybrids have chromosome bridges, showing they are heterozygous for inversions. In hybrids of species with *n* = 20 or lower the number of paired elements (bivalents and multivalents) at meiosis approaches or equals the number of chromosomes from the parent having the smaller number, and it never exceeds this. As in *Echeveria* (Uhl, 1992) and Mexican *Sedum* (Uhl, 1985), we believe this shows that pairing in these hybrids occurs only between chromosomes from the two parents, which means that both parents are effectively diploid.

We believe that over time a series of translocations has rearranged the ancestral genome of *Villadia* into progressively fewer but larger chromosomes, from *n* = 21, or probably even more, down to *n* = 9. Thus *Villadia,* like *Echeveria* (Uhl, 1992), has come to have a long descending series of dysploid chromosome numbers. Both in *Villadia* and in *Echeveria* the series of consecutive dysploid numbers is much longer than has been reported elsewhere (Grant, 1975) and the numbers start much higher; but note that species with all numbers in the series behave cytologically as effective diploids.

In *Sedum* species formerly in *Altamiranoa* we have found gametic chromosome numbers of 20, 23, 25, 28, 29, and several higher, evidently polyploids. The species appear most similar, morphologically and cytologically, to *Sedum* section FRUTICISEDUM Berger (*n* = 26–31, Uhl, 1980), from which they are probably derived. As in *Villadia,* they are dysploid, but their generally higher chromosome numbers suggest they have changed less from their ancestors.

These observations suggest something of how *Villadia* and relatives may have evolved: (1) *Villadia* and especially the *Altamiranoa* group of *Sedum* appear closest to subshrubby species of *Sedum* section FRUTICISEDUM. Those species have gametic chromosome numbers of 26 to 31, and hybrids of six of them show that none of their chromosomes can pair with each other and thus that they are effectively diploid (Uhl, 1980). (Although these high numbers appear to be diploid now, they may have arisen long ago as polyploids from unknown diploid ancestors, but there is no direct evidence for this.) (2) These plants generally grow in pioneer habitats such as cliffs and lava, often as small and ephemeral populations, allowing opportunity for new forms to establish themselves locally. (3) Over time many translocations and inversions have rearranged the basic genome into ever fewer but larger units, as Uhl (1992) suggested for the long descending dysploid chromosome series in *Echeveria.* (4) These changes would restrict genetic interchange between plants with the original and those with the new karyotype, helping to isolate them reproductively from each other. (5) More genes become linked together, but into fewer groups; those in new chromosomal neighborhoods are likely to be activated at different times during development, which could affect the appearance of the plant. (6) With generally fewer and larger chromosomes, *Villadia* seems to have changed more from its supposed *Sedum* ancestors than have species of *Sedum* of the *Altamiranoa* group.

Although we know of no natural hybrids of *Sedum* species with *Villadia,* there are three probable natural hybrids with other *Sedum* species formerly in *Altamiranoa.*

(1) *Sedum* (X*Sedadia*) *amecamecanum* is apparently a hybrid between *Sedum praealtum* DC (n = 34) and *Sedum goldmanii* (= *Villadia* = *Altamiranoa batesii*) (n = 25) (Clausen, 1959; Uhl, 1978). It has been found in nature only with its putative parents, and it is meiotically irregular and sterile. (2) For two localities near Tlaxcala Clausen (1959) reported sterile hybrids intermediate between *Sedum quevae* Raym.-Hamet (n = 20) and what he called *Villadia scopulina* Rose (= *Sedum scopulinum*) but what evidently was *S. goldmanii* (n = 25). (3) A third probable hybrid (*UC54.170*) was grown by Eric Walther, who said he collected it at 4250 m on Nevado de Toluca. Distributed by the International Succulent Institute (number 151) as *Villadia batesii*, it has caused much confusion in Europe regarding that common species (R. Stephenson, in litt.). Clausen (1959) thought it a possible hybrid between *Sedum moranense* and *V. batesii* (= *S. goldmanii*). This parentage is improbable, because *S. goldmanii* is unknown in the area. However, hybrid status is supported by its extreme irregularity at meiosis (24–27 paired elements plus 3–14 univalents in eight cells analyzed) and by its abortive pollen (Uhl, 1983).

Despite the rarity of natural hybrids, Uhl (1994) has made 15 different hybrids by crossing eight species of *Villadia* or *Sedum* (formerly in *Altamiranoa*) in various combinations with nine species of other Mexican genera (*Cremnophila, Echeveria, Graptopetalum, Pachyphytum,* and *Sedum*). Species he crossed were *V. albiflora* (n = 15), *V. aperta* (n = 15), *V. guatemalensis* (n = 20), *V. nelsonii* (n = 20), and *V. recurva* (n = 14), and *S. jurgensenii* (n = 23) and *S. grandisepalum* (n = 44) as well as *S. latifilamentum* (n = 20). He also made four hybrids between different species of *Villadia* and three between species of *Villadia* and species of *Sedum* formerly in *Altamiranoa.* The chromosome number of the second parent ranged from n = 18 to n = 34, and for each hybrid the two parents had different chromosome numbers. We cite the hybrids above in the discussions of their parental species. Doubtless with a little patience and luck, many other species of *Villadia* could be interconnected.

In most intergeneric hybrids of *Villadia* fewer chromosomes paired than in most other intergeneric hybrids of the Mexican Crassulaceae (Uhl, 1994), perhaps suggesting a more distant relationship. In each intergeneric hybrid the *Villadia* had fewer chromosomes than the other parent, and often these were noticeably larger and could therefore be distinguished at metaphase I in the hybrids studied (e.g., Figs. 39–43).

The South American species are poorly known, and our sample of them is very small. Three that we studied, *Sedum* ?*grandyi* (n = 38, probably), *S. andinum* (n = 40–48) and *S.* sp. (n = ca. 50), have been placed in *Altamiranoa,* but we reassign them to *Sedum,* where they were originally named. Their chromosome numbers suggest that they are polyploid, but they are more irregular at meiosis than polyploids of Mexican genera (Uhl, 1992), and our plants may have been hybrids or possibly odd-ploids. *V. incarum,* with a racemose inflorescence, is perhaps a true *Villadia.* Plants under this name have n = 88–89, with normal meiosis.

Geographically and cytologically, the Crassulaceae of South America (aside from *Crassula*) fall into two groups, with little or no overlap. We have no records of *Villadia* or *Sedum* from Venezuela, Colombia, or Ecuador, but more than 60 collections of *Echeveria* from these countries had n = 21 or n = 22, with also a triploid and several tetraploids based on these numbers (Uhl, 1993, and unpublished data). These echeverias from northern South America have an almost continuous range of forms, and delimitation of species is difficult. They give a clear impression of a single group that has recently arrived and is evolving rapidly to occupy a variety of ecological niches.

Our most northerly records of *Villadia* and *Sedum* in South America are from northern Peru. Our small sample of these plants appears to be entirely polyploid, with gametic numbers from 38, probably, to 89, and most were irregular at meiosis. Our collections of *Echeveria* from these countries likewise were all polyploid. Two tetraploids with n = 44 from extreme northern Peru resembled the species from farther north. However, all 25 collections of *Echeveria* from farther south in Peru and from Bolivia and northern Argentina appeared quite different from the northern plants, and they had n = 50 or more (Uhl, unpublished data). In fact, 15 of these collections had *gametic* chromosome numbers from ca. 120 to 260. Many also were in some degree irregular at meiosis.

Villadia, *Sedum* (formerly *Altamiranoa*), and *Echeveria* are all clearly centered in Mexico and must have originated there. We suppose that Crassulaceae may have entered South America at least twice from the north. The first immigrants are represented now by the polyploids of *Echeveria*, *Villadia*, and *Sedum* that occur from Peru southward. Much more recently a single species of *Echeveria* must have entered South America from the north and have evolved rapidly in Venezuela, Colombia, and Ecuador; but apparently no villadias or sedums came with it.

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