

CHROMOSOMES AND HYBRIDS OF *Echeveria* DC. IX. SERIES SPICATAE (BAKER) BERGER

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Abstract: Eric Walther classified three generally epiphytic species in his series Spicatae of *Echeveria*. Two of these, *E. rosea* ($n = 34$) and *E. pittieri* ($n = 62$) are distinctive, but *E. chiapensis* is not distinguishable from *E. rosea*. Certain plants from Oaxaca and Veracruz closely resemble *E. rosea* vegetatively but differ in the form of their flowers, and they have $n = 51$ or $50 + 1$. We describe them here as a new species, *E. tencho*. All three species hybridize readily with many other Mexican Crassulaceae in cultivation.

Although we first thought that *E. rosea* was a tetraploid and *E. tencho* a hexaploid having a common ancestor with $n = 17$, analysis of chromosome pairing in their hybrids with other species requires a different interpretation. At meiosis in its hybrids none of the 34 gametic chromosomes from *E. rosea* can synapse with any of its others, although many synapse with parts of one or more chromosomes from the other parent. They are all different, and, like many other Mexican Crassulaceae that have this many chromosomes, *E. rosea* is effectively diploid. The behaviour of the 50 or 51 chromosomes from *E. tencho* at meiosis in its hybrids suggests that it may be a diploidized descendant of autotetraploid ancestors with $n = 50$, which were in turn derived from diploids with $n = 25$. *E. pittieri* appears to be an allotetraploid, but its ancestors are not known. The species of Walther's series Spicatae appear to be much less closely related than the similarities in their appearance and habitat suggest.

Key words: Crassulaceae, cytogenetics, *Echeveria*, *Echeveria pittieri*, *Echeveria rosea*, *Echeveria tencho* sp. nov., hybrids, hybridization, polyploidy, Series Spicatae.

Introduction

In his posthumous monograph of *Echeveria*, Eric Walther (1972) grouped three caulescent species into series Spicatae based on their generally epiphytic habit and their densely congested spikes or racemes. Species of series Nudae and Elatae are also caulescent and not very distinct from the Spicatae, but none of them are primarily epiphytic and their flowers are generally less crowded. Although species of series Mucronatae and Racemosae differ in their acaulescent habit, some of them seem otherwise not very distinct from series Spicatae. Probably these series do not all represent natural groups. Certain plants from Oaxaca and Veracruz closely resemble *E. rosea* vegetatively but differ in the form of their flowers and chromosome number. We describe them here as a new species, *E. tencho*.

Materials and Methods

Slides were prepared as before (Uhl, 1992), and photographs of chromosomes are from marked cells on permanent slides. Interpreta-

tions of univalents, bivalents and multivalents are based on their size and their depth of focus under the microscope and are believed accurate within one or two. Herbarium specimens of parents and hybrids are in the Bailey Hortorium of Cornell University.

Results

I. *Echeveria rosea*

Echeveria rosea Lindley (1842) was the first species of series Spicatae to be named. It was based on plants imported into England from an unspecified locality in Mexico, and an excellent drawing, reproduced without color (Walther, 1972, Fig. 176), leaves no question regarding the plant. Lemaire (1851) mistakenly thought its flowers have a staminal tube and lack nectaries, and he placed *E. rosea* into a new genus, *Courantia*. Britton and Rose (1905) retained *Courantia* in their monograph, but Walther (1935) noted that flowers of *E. rosea* do not really have a staminal tube and that they do indeed have small nectaries; he therefore returned the spe-



Figure 1A. *E. rosea* (Kimmach, Cházaro, Dorsch & Negrete 3278B, Chiapas, 4 km from the Pan-American Highway on road to Ocosingo). Photo: Kimmach. **Figure 1B.** *E. rosea* (Moran & Kimmach 7763). Photo: Moran. **Figure 1C.** *E. rosea* (Baker et al., Querétaro), with more widely spaced flowers. Photo: Kimmach.

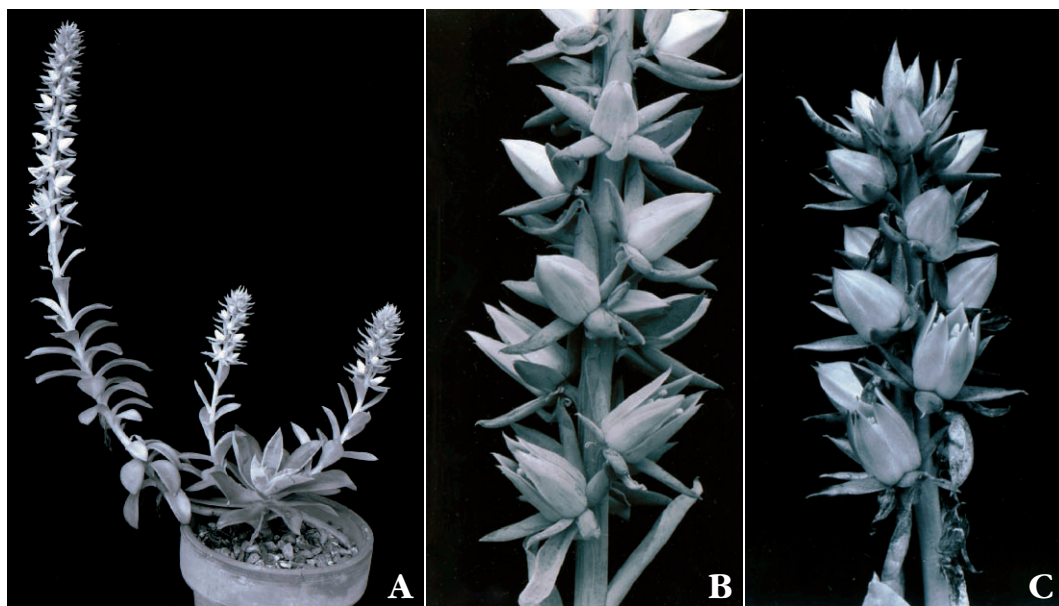
cies to *Echeveria*.

Based on Matuda's (1963) description and photo, *E. omilt-emiana* does not appear distinguishable from typical *E. rosea*, although it came from Guerrero, far to the west of any plants like this that we have studied.

Echeveria rosea is usually epiphytic and is native to mountains in eastern Mexico from San Luis Potosí to Chiapas, where humid air from the Gulf of Mexico flows inland over mountain ridges. It is caulescent, with leaves distributed rather densely along the upper part of the stem, and its flowers are nearly always crowded in tight, lateral racemes or spikes (in Baker et al. 6096, from Querétaro [Fig. 1c], they are more diffusely separated on the rachis). The sepals are very narrow, erect and as long as—or longer than—the petals (Figs. 1a–1c, 9). Some plants have bright red bracts and sepals, while in others their color is duller. The petals are pale yellowish, often tinged a little reddish.

In our collections of epiphytic echeverias we early noted two forms in Mexico that are very similar in their vegetative form but differ consistently in the shape and degree of expansion of their sepals, their weaker coloring, their chromosome numbers, and in other ways. One form has linear, erect sepals crowded against the corolla and at least as long as the petals; it closely conforms to the original description and drawing of *Echeveria rosea* (Lindley, 1842). Walther (1972, p. 229) published a color photo of one of our plants of this form. We have studied living plants of 19 collections like this (Figs. 1A–1C), ranging from San Luis Potosí to Chiapas. All twelve of these that were studied cytologically had $n = 34$ (Appendix 1, Fig. 14).

The second form—published below as *E. tencho*—is represented by seven collections with sepals that are broader, more or less lanceolate, distinctly shorter than the petals, and that spread from the base of the corolla at a 25 to



Figures 2A–C. *E. tencho*. Photos: Moran. **A.** (type collection, MacDougall B-266). **B.** Closeup of lowers in 2A. **C.** Flowers (MacDougall B-11, Tenango, Oaxaca; U498).

Figure 3. *E. rosea* (Moran 7815, $n = 34$) \times *E. coccinea* (Moran 7788, $n = 25$). Photos 3–31: Uhl



45 degree angle (Figs. 2a–2c). Six of these collections had 51 pairs of chromosomes (Fig. 15), and the other, slightly different, had $n = 50$ plus a small, extra chromosome. Leaves of these plants are generally less lax than those of the true *E. rosea*, although this character appears variable, and when they are not in flower we are not sure that we can always distinguish the plants from *E. rosea*.

In 1904 J. N. Rose wrote the name *Echeveria chiapensis* on a herbarium sheet of his collection 1011 but added no further information as to its origin. However, Moran (1972) noted that Rose listed this collection in his greenhouse notebook as Goldman's 964, coming from 20 miles SE of Teopisca, Chiapas. Rose never published the name, but Poellnitz (1936) cited this collection as the type of his new *E. chiapensis*, describing it as having sepals that are as long as the corolla and pressed against it ("angedrückt"). Thus, in these critical characters *E. chiapensis* resembles typical *E. rosea*. In spite of this, for a long time we assumed that our second form (*E. tencho*) was *E. chiapensis*.

In his monograph, Walther (1972) based his description of *E. chiapensis* on living plants from Lago Montebello, Chiapas, yet we consider that his description fits typical *E. rosea* very well. Although we have not seen living plants from this locality, two of our collections came from other places in Chiapas (Appendix 1), one of them about 50 km from the type locality



Figure 4. *E. rosea* (UC51,642, $n = 34$) \times hairy *E. setosa* var. *ciliata* (Moran 7733, $n = 25$). Note hairs on pedicels. **Figure 5.** *E. rosea* (Moran 7815, $n = 34$) \times *Pachyphytum viride* (Moran 10179, $n = 33$). **Figure 6.** White-flowered *Sedum cuspidatum* (U1263, $n = 34$) \times *E. rosea* (Moran 10068, $n = 34$).

of *E. chiapensis*. Both of these also are typical *E. rosea*, and both had $n = 34$. None of our collections of *E. tencho* came from Chiapas. In his key, Walther distinguished *E. chiapensis* first by its very short pedicels as opposed to those of *E. rosea*, in which they are up to 5 mm long.

We find pedicel length much too variable and unreliable a character; the lengths of the pedicels in our herbarium specimens range from 0 to 10 mm in *E. rosea* and from 4 to 14 mm in *E. tencho*.

Walther (1972) also stated that he found *Echeveria chiapensis* near Esperanza, Puebla, in 1957. The next year he sent Uhl a plant under this name that he said was collected there by Thomas MacDougall (*B-11* = *U676*). He also published a photograph (his Fig. 175) of a plant that he said Purpus had collected there earlier, identifying it as *E. chiapensis*. The photograph shows sepals that are long, narrow and erect. The plant that Walther sent to Uhl (*U676*) also has these characters and has $n = 34$. These are all characters typical of *E. rosea*.

As further indication of Walther's confusion, a year earlier, in 1957, Uhl had received directly from MacDougall a different plant as *B-11* (= *U498*), with the information that it came from Tenango, in the Chontal region of Oaxaca. We consider that this latter plant, coming directly from MacDougall, is the genuine *B-11*, and it is *E. tencho*, with shorter, spreading sepals and $n = 51$. Walther (1972) based his citation of $n = 51$ for *E. chiapensis* on this plant.

Thus we consider Walther's treatment of these species to be highly unsatisfactory, and we believe that *E. chiapensis*, as originally described, is the same as typical *E. rosea*. Kimnach (2003) agrees and combines it with *E. rosea*. The form with 51 pairs of chromosomes and shorter, broader, spreading sepals is here-with described as *E. tencho*.

II. *Echeveria tencho* Moran & Uhl sp. nov.

Planta fruticosa, caulibus ad 15 cm longis vel ultra, 8–15 mm crassis, foliis subdiffusis, oblanceolatis acutis viridis vel rubellis 5–6.5 cm longis 15–22 mm latis apicem versus, 3–4 mm crassis; caules florens ad 5 dm longi 6 mm crassi, foliis ellipticis ad oblanceolatis 2.5–4 cm longis 11–17 mm latis; racemi 7–20 cm longi 3.5–4 cm lati; pedicelli 2–3 mm longi; sepala expansa 6–12 mm longa 2–4 mm lata; corolla 13–15 mm longa 9–11 mm crassa flavida, rubella versus apicem, petalis triangularibus 3.5 mm latis. Chromosomatum numerus: $n = 51$.

Type Locality: on *Pachira aquatica*, Catemaco, just E of San Andrés Tuxtla, Veracruz, Mexico (near 18°25'N, 95°07'W), ca. 390 m, December 15, 1965, *Thomas MacDougall* B266, flowering in San Diego January 13, 1967 (Moran 13277).

Holotype: SD 130060.

Etymology: *tencho* = an epiphytic plant

Plant shrubby. Caudex branching, to 5 dm tall or more, 8–15 mm thick, pale green

Table 1. Chromosome pairing in hybrids. A species preceded by an × was the pollen parent, one followed by an × was the seed parent.

Hybrids of <i>E. rosea</i> , <i>n</i> = 34 (Moran 7815 and 10068, Uhl 1861, and UC51.642)						
Second parent	<i>n</i> =	Hybrid	Bi- and multi-valents	Univalents	Cells	Figure
× <i>E. pulvinata</i>	23	<i>M7815</i> × <i>U1204</i>	22-23	2-8	11	17
× <i>E. setosa ciliata</i>	25	<i>UC51.642</i> × <i>M7733</i>	22-25	2-9	20	18
× <i>E. coccinea</i>	25	<i>M7815</i> × <i>M7788</i>	24-25	0-3	10	19
<i>E. sp. cf. fulgens</i> ×	27	<i>U2138</i> × <i>U1861</i>	22-27	6-15	11	20
<i>Pachyphytum bookeri</i> ×	32	<i>M13349</i> × <i>U1861</i>	30-32	0-4	16	21
× <i>P. viride</i>	33	<i>M7815</i> × <i>M10179</i>	28-32	1-6	5	
<i>Sedum cuspidatum</i> ×	34	<i>U1263</i> × <i>M10068</i>	32-34	0-4	18	22
<i>S. lucidum</i> ×	34	<i>U1462</i> × <i>M10068</i>	32-34	0-4	29	23
× <i>E. leucotricha</i>	38	<i>M7815</i> × <i>U1203</i>	19	14-30	10	24
× <i>E. pulidonis</i>	62	<i>UC51.642</i> × <i>UC61.589</i>	30-31	19-29	9	
× <i>P. glutinicaule</i>	66	<i>M7815</i> × <i>M7805</i>	ca. 33	27-30	5	
Hybrids of <i>E. tencho</i> , <i>n</i> = 51 (U498, Moran 13754, or UC58.847)						
× <i>E. coccinea</i>	25	<i>U498</i> × <i>M7788</i>	24-25	5-14	10	29
<i>Graptopetalum fruticosum</i> ×	31	<i>U1398</i> × <i>M13754</i>	23-30	14-27	15	25
<i>Pachyphytum bookeri</i> ×	32	<i>M13349</i> × <i>M13754</i>	22-32	11-31	14	26
× <i>P. viride</i>	33	<i>UC58.847</i> × <i>M10179</i>	24-32	8-26	10	27
<i>Cremnophila nutans</i> ×	33	<i>M10174</i> × <i>M13754</i>	29-33	3-13	17	
<i>E. pittieri</i> ×	62	<i>UC57.238</i> × <i>UC58.847</i>	38-51	0-6	10	28
Hybrids of <i>E. tencho</i> , <i>n</i> = 50 + 1 (U2665)						
× <i>E. pulvinata</i>	23	<i>U2665</i> × <i>U2367</i>	46-49 elements		6	
<i>E. cf. steyermarkii</i> ×	28	<i>U2596</i> × <i>U2665</i>	23-30	11-32	14	
<i>E. globuliflora</i> ×	42	<i>U500</i> × <i>U2665</i>	46	0	6	
Hybrids of <i>E. pittieri</i> , <i>n</i> = 62 (U2590, UC57.238)						
× <i>E. australis</i>	28	<i>UC57.238</i> × <i>UC57.021</i>	31	10	1	30
× <i>E. secunda</i>	32	<i>U2590</i> × <i>U2352</i>	39-44	1-14	26	
× <i>E. tencho</i>	51	<i>UC57.238</i> × <i>UC58.847</i>	46-51	0-6	10	
<i>Pachyphytum bookeri</i> ×	32	<i>M13349</i> × <i>U2590</i>	7-27	34-78	10	31

and glaucous above, darker below, leaf scars lenticular, 5–6 mm wide, ca. 0.5–1 mm high. Terminal rosette rather diffuse, 7–12 cm wide; **leaves** 12–25, oblanceolate, broadly acute and submucronate, 5–6.5 cm long, 15–22 mm wide above, 6 mm wide at base, 3–4 mm thick, at first ventrally channeled but later flattish, somewhat glaucous when young, later green or becoming reddish, **Floral stems** 1–3, originating from among rosette leaves but below rosette by anthesis, to 5 dm tall, 6 mm thick, leafless along basal 3 cm, with 15–50 leaves above; stem leaves ascending at base but outcurved, elliptic to oblanceolate, broadly acute, apiculate, spurred, the largest 2.5–4 cm long, 11–17 mm wide, 2.5–3 mm thick, green, glaucous; **racemes** 7–20 cm long, 3.5–4 cm wide at anthesis, with 25–40 flowers, the internodes ca. 5 mm long, rarely with a 2-

flowered branch; **bracts** linear-lanceolate, acuminate, spurred, often withering before anthesis, green, 11–15 mm long and 2–4 mm wide, slightly glaucous, tips of bracts and sepals (and especially young bracts at apex) slightly colored; **pedicels** 2–3 mm long, ca. 1–1.5 mm thick, **bracteoles** much smaller than bracts, ca. 3–5 mm long; **calyx disc** 4–5 mm wide, light green, slightly glaucous, **sepals** widely spreading but slightly ascending, unequal, triangular-lanceolate, acuminate, 6–12 mm long, 2–4 mm wide; **corolla** pentagonal in bud, 13–15 mm long, 6–7 mm thick at base, 9–11 mm thick above, light yellow somewhat tinged with rose on apical half, the tube 1.5 mm long, petals slightly divergent, not in contact in upper two-thirds, straight, triangular-lanceolate, narrowly acute, apiculate, 3.5 mm wide, less than 1 mm thick, obtusely keeled, shallowly chan-



Figure 7. Triploid hybrid: *E. rosea* (UC51.642, $n = 34$) \times tetraploid *E. pulidonis* (UC61.589, $n = 62$). **Figure 8.** Triploid hybrid: *E. rosea* (Moran 7815, $n = 34$) \times tetraploid *Pachyphytum glutinicaule* (Moran 7805, $n = 66$). **Figure 9.** Pairs of flowers: *E. rosea* (Moran 7815, $n = 34$) (left), Tetraploid *P. glutinicaule* (Moran 7805, $n = 66$) (right) and their triploid hybrid (center).

neled ventrally, slightly cupped at base but scarcely excavate; **filaments** ca. 7 mm long from corolla base, 0.8–0.9 mm thick, the epipetalous adnate for ca. 3 mm, the antese-palous adnate for ca. 2 mm, extending higher, pale yellow; **anthers** oblong, light yellow, 2.5–3 mm long, 1 mm wide; nectaries yellow, 1.4 mm wide, 0.5 mm thick; **gynoecium** 7–8 mm high, 4–4.5 mm thick, pistils erect but

slightly separated, connate for ca. 1 mm, ovaries white, tapering gradually into indefinite styles; styles ca. 3 mm long, yellowish slightly tinged with red; ovules ca. 170, ca. 0.55–0.65 mm long; young follicles still erect but later well-separated, ca. 10 mm long, thicker below; immature **seeds** 0.6–0.9 mm long, 0.3 mm thick, papillose. **Chromosome numbers:** $n = 51$, $n = 51 + 1$.

Distribution: MEXICO. Oaxaca: Road cut on Mex. 175, 16 km NE of Valle Nacional, 2750', *J. Bauml* & *M. Kimmach* 486 (HNT), (= *C. H. Uhl* 2665, BH); Mex. 175, between Tuxtepec and the city of Oaxaca, 750 m alt., *J. Meyran s. n.*, *Huntington B. G.* 44951 (HNT); in soil, Cerro Guajinicuil, Santiago Guevea, 920 m, *UCBG* 58.847, *T. MacDougall B-202* (BH); same locality, *UCBG* 58.861 (BH); Agua Zarca, Santiago Lachiguiri, *R. Moran* 13754 (*T. MacDougall B-276*) (BH, HNT); epiphytic, Tenango, 1525 m, *C. H. Uhl* 498 (*T. MacDougall B-11*); cultivated, *UCBG* 56.1277 (BH). Veracruz: on roof-tops, San Andrés Tuxtla, 300 m, *M. Sousa* 3415 (SD).

Mario Sousa Sánchez collected paratype plants of *E. tencho* in other vegetation growing on roof-tops in San Andrés Tuxtla, Veracruz, just west of the type locality. He noted that the local people referred to the echeveria as a *tencho*, a word applied generally to any epiphytic plant, including orchids, bromeliads and ferns. We are utilizing the word as the specific name for our new species, although the latter is not always epiphytic—as with *E. rosea*, any well-drained substratum will suffice as a perch: roof-tops, the sides of cliffs, and steep road-cuts.

In the coffee plantations of Veracruz it is a common practice to strip all the epiphytes from coffee plants because of a belief that they are parasites or that the shade they cast will harm the crop. “Destenche” is a vernacular word for the process of removing “tenchos” (Anon., n.d.).

At the present time there seems to be only a single collection of *E. tencho* in cultivation in the United States, that collected by Bauml and Kimmach in 1981. In the ensuing 24 years, it seems to have become afflicted with a virus and no longer flowers or produces healthy

growth. It is therefore not being propagated for further distribution.

III. *Echeveria pittieri*

The third species of Walther's series *Spicatae* is *Echeveria pittieri* of Central America. This species and most of its hybrids have been discussed previously (Uhl, 2004). It resembles *E. rosea* in its crowded inflorescence and often epiphytic habit, differing in its pinkish flowers and more spreading sepals. Our three collections, all from Guatemala, had $n = 62$ (Fig. 16).

Discussion

Cytological Observations

Every gametic chromosome number from 12 to 34, as well as many higher numbers, has been found in *Echeveria* (Uhl, 1992). It is very difficult to determine how these many numbers evolved and to identify the numerical boundary between diploid and polyploid species. At first glance it would appear that *E. rosea* with $n = 34$ and *E. tencho* with $n = 51$ represent tetraploid and hexaploid descendants from a common ancestor with $n = 17$. One approach to this problem is to produce hybrids and study how their parental chromosomes pair at meiosis. This offers measures of the similarity of the parental chromosomes and the relationship of the parental species.

Chromosome pairing at meiosis (synapsis) occurs only between closely corresponding (homologous) chromosomes, or parts of chromosomes, and once it occurs a third chromosome is not attracted in that region. However, if there are sites in a chromosome where the homology switches to a different chromosome, then configurations involving three or more chromosomes (multivalents) can result. Most hybrids of *Echeveria* have multivalents at meiosis, often many and/or large ones. This indicates that the genetic sequences in many chromosomes have been rearranged during evolution.

After meiosis, diploid species pass only one chromosome of each kind to their progeny. Thus the *only* chromosomes that can synapse in hybrids between two diploids are those that came from the *different* parents. This restricts the number of their paired chromosomal elements (bivalents plus multivalents) at meiosis in their hybrids to the number of chromosomes that came from the parent with fewer chromosomes. Many hundreds of hybrids of *Echeveria* and related genera exhibit this restriction. *Every* chromosome number from $n = 12$ to $n = 34$ occurs in their parental species, so all of the species



Figure 10. *Cremonophila nutans* (Moran 10174, $n = 33$) \times *E. tencho* (Moran 13754, $n = 51$).

must therefore be considered to be effectively diploid. Apparently they are descended from one common ancestor whose genome has become extensively rearranged during evolution into these many different numbers of parcels (chromosomes). Despite these changes in genetic sequence and chromosome numbers, many of their rearranged parts still have enough homology for each other that they can synapse.

Tetraploids have four outfits of chromosomes, and after meiosis they contribute two of them to their progeny. *Echeveria* and related genera have many tetraploids and higher polyploids, some with chromosome numbers higher than $n = 200$, and these also hybridize freely (Uhl, 2003). Cytologically they are difficult to study because their multiple homologues often change partners as they pair, producing multivalent associations. In hybrids among the Mexican Crassulaceae, the two corresponding chromosomes of each kind that come from a tetraploid parent are the most similar to each other, and they pair preferentially with each other at meiosis. Apparently their synaptic attraction is much stronger for each other than it is for any chromosomes, or part of chromosomes, from the other parent. This characteristic of pairing is conspicuous after several of their hybrids have been studied (Uhl, 1992, 1995). This defines these parents as autopolyploids: they have four or more *very similar* chromosomes of each kind, and any two of them can synapse equally well at meiosis. (The same behavior also occurs in *Echeveria* species of higher ploidy.)

Thus, in these plants the rules regarding chromosome pairing in hybrids between diploid parents are very different from those in hybrids between tetraploids. Diploid hybrids, by definition, have only one chromosome of each kind, although the chromosomes of the different parents usually have some parts that are homologous. Pairing in them occurs only between chromosomes, or corresponding segments of chromosomes, from the *different* parents. On the other hand, autotetraploid parents contribute two very similar chromosomes of each kind to their hybrids, and chromosomes from the



11



12

same parent there form pairs preferentially.

With a single outfit of chromosomes and genes from each parent, hybrids between diploid species generally appear like a compromise, midway between the appearance of their parents (Figs. 3–6). Hybrids between a diploid and an autotetraploid are triploid. They receive a double dose of genetic information from their tetraploid parent, and they resemble it more closely (Figs. 7–9). This shows that the multiple genomes of polyploids are all active in their hybrids.

Species and hybrids

As noted above, our first impression was that plants with $n = 34$ (*Echeveria rosea*) are tetraploids and those with $n = 51$ (*E. tencho*) are hexaploids, both derived from an unknown diploid ancestor with $n = 17$. Unfortunately we made no hybrids between these two species, but cytological analysis of other hybrids requires a different interpretation.

Hybrids were made between typical *Echeveria rosea* ($n = 34$) and eight diploid species of three genera: *E. pulvinata* ($n = 23$), *E. coccinea* ($n = 25$) (Fig. 3), *E. setosa* var. *ciliata* ($n = 25$) (Fig. 4), *E. sp. ser. Gibbiflorae* ($n = 27$), *Pachyphytum hookeri* ($n = 32$), *P. viride* ($n = 33$) (Fig. 5), *Sedum cuspidatum* ($n = 34$) (Fig. 6) and *S. lucidum* ($n = 34$). All of the hybrids are nicely intermediate between their parents. Most of their chromosomes synapse for at least part of their length at meiosis, but most cells have several multivalents and generally one or a few unpaired chromosomes (univalents) (Table 1, Figs. 17–23). In each of these hybrids the number of paired elements closely approaches or equals the number of chromosomes that came from the parent with fewer chromosomes, whether it was 23, 25, 27, 32 or 33, and it never exceeds this (Table 1). The best explanation for this pattern of synaptic pairing is that it occurs *only* between chromosomes of the *different* parents (Uhl, 1982). Apparently none of the 34 chromosomes from *E. rosea* are able to pair with each other in its hybrids, although most of them, or parts of them, pair substantially with chromosomes from the other parent. This pattern is seen in many hundreds of other hybrids of *Echeveria*, and it defines *E. rosea* as effectively diploid.

If we accept this, then hybrids between *Echeveria rosea* and three definitely autotetraploid species are triploid. These hybrids all appear more like their tetraploid parents (Figs. 7–9). For example, *E. rosea* is glabrous, and its hybrid as seed parent with the hairy autotetraploid *E. leucotricha* ($n = 38$) is triploid, and it has the hairy stems, leaves and flowers of its

Figure 11. *Graptopetalum fruticosum*, (U1398, $n = 31$) *E. tencho* (Moran 13754, $n = 51$). **Figure 12.** Same. Flowers.



Figure 13. *E. tencho* (UC58,847, $n = 51$) \times *P. viride* (Moran 10179, $n = 33$). Compare Figure 5.

pollen parent. From its autotetraploid parent, *E. leucotricha*, this hybrid received two chromosomes each of 19 kinds that are fully homologous. These chromosomes synapse preferentially with each other at meiosis, and all ten cells analyzed had 19 paired elements (Fig. 24). These same cells also had 16–30 unpaired elements, representing most of the chromosomes from *E. rosea*. Parts of the others from *E. rosea* synapse with homologous parts of one of the chromosomes of a pair from *E. leucotricha* to form multivalents.

The inflorescence of the triploid hybrid between diploid, racemose, pale-flowered *E. rosea* ($n = 34$) and autotetraploid, cincinnate *E. pulidonis* ($n = 62$) is a bifid cincinnus, and it has the bright yellow flowers of its staminate parent (Fig. 7). In nine cells that could be analyzed at metaphase I of meiosis, it formed 30–31 paired elements, representing the 62 chromosomes that came from *E. pulidonis* (some with chromosomes from *E. rosea* attached by homologous segments) and 19–29 unpaired elements, representing most of the 34 chromosomes from *E. rosea*. The hybrid between *E. rosea* and the cincinnate, autotetraploid *Pachyphytum glutinicaule* ($n = 66$) also produced a bifid cincinnus (Fig. 8), and its flowers were shaped more like those of its *Pachyphytum* parent (Fig. 9). At meiosis it produced about 33 paired and 27–30 unpaired elements.

All three of these triploid hybrids resemble their autotetraploid parent more closely than they do *E. rosea*, and the number of paired chromosomal elements (multivalents plus bivalents) at meiosis very closely matches half the number of chromosomes from each of their autotetraploid parents (Table 1). The large numbers of unpaired chromosomes (univalents) represent most of the 34 chromosomes of the single set that each hybrid received from its diploid *E. rosea* parent. Although some parts of the *E. rosea* chromosomes are homologous with parts of those from the autotetraploid parent, most pairing occurs preferentially between

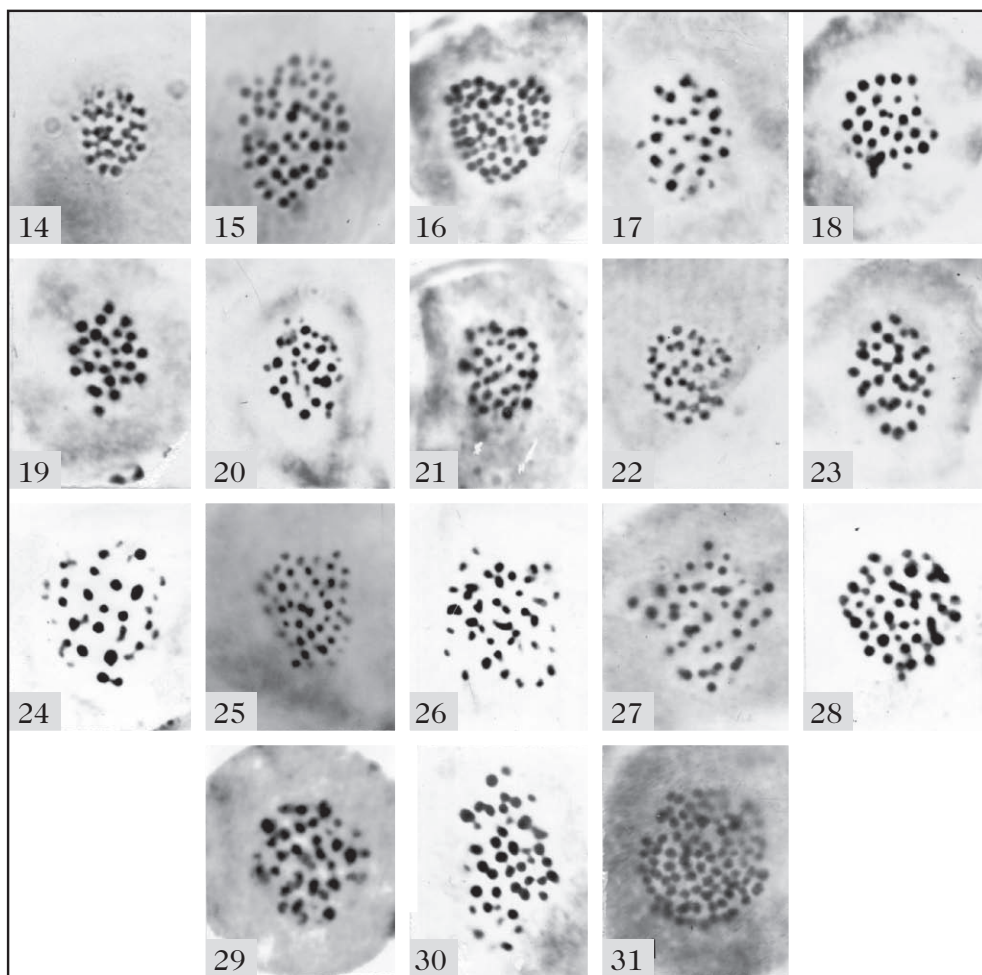
the much more similar chromosomes of the two sets from the tetraploid parent (Uhl, 1982, 1995). Only two chromosomes can synapse at any one site, and in these triploid hybrids this preempts most heterologous pairing between chromosomes from the different parents. The chromosomes from *E. rosea* in the hybrids are all different, one each of 34 kinds. None of them can pair with any of the others and most remain unpaired as univalents. Pairing between any of them would result in more paired elements than were observed.

We believe that the appearance of the plants and the behavior of the chromosomes at meiosis in hybrids between *E. rosea* and other species, both diploid and tetraploid, offers convincing evidence that *E. rosea* must be considered to be effectively diploid, regardless of how it may have arisen in the past. We see no evidence that would support its origin from a recent ancestor with $n = 17$.

Evidence regarding the ploidy of *E. tencho* is not so clear. Mexican Crassulaceae with this many gametic chromosomes are generally autotetraploids, and at meiosis they usually form some multivalents, which makes it difficult to determine their true number. Multivalents do not occur in *E. tencho*, and chromosomes can therefore be counted easily despite their number. Hybrids of tetraploids with diploids are triploids, and they look more like their tetraploid parents. Hybrids between *E. tencho* and five species that test as diploids in their many other hybrids, *Cremnophila nutans* ($n = 33$) (Fig. 10), *Echeveria coccinea* ($n = 25$), *Graptopetalum fruticosum* ($n = 31$) (Figs. 11, 12), *Pachyphytum bookeri* ($n = 32$), and *P. viride* ($n = 33$) (Fig. 13), all have a closer resemblance to *E. tencho*. This is evidence that the plants with $n = 51$ are tetraploids of some sort.

The corresponding chromosomes of the two sets from an autotetraploid parent pair preferentially with each other at meiosis in its hybrids. However, in these same five hybrids the chromosomes behave at meiosis more like they do in hybrids between two diploid species. Most cells had some large multivalents (Figs. 25–27, 29), but none of them had more paired elements at meiosis than the 25 to 33 chromosomes it received from its lower-numbered parent (Table 1).

Hybrids of one other collection (U2665) offer a clue to this problem. U2665 differs slightly in appearance from the other plants of *E. tencho*, and it has $n = 50$ plus a very small unpaired chromosome. Its hybrid as pollen parent with autotetraploid *E. globuliflora* ($n = 42$) formed 46 pairs of chromosomes in all six cells that could be analyzed at metaphase I of meiosis. Apparently two sets of 21 chromosomes each from *E. globuliflora* form pairs preferentially with each other in the hybrid, as expect-



Chromosomes of Species and Hybrids at Metaphase I

Figure 14. *Echeveria rosea*. Moran 7813, $n = 34$. **Figure 15.** *E. tencho* U498, $n = 51$. **Figure 16.** *E. pittieri*. U2590, $n = 62$. **Figure 17.** *E. rosea* (Moran 7815, $n = 34$) \times *E. pulvinata* (U1204, $n = 23 + 1$). 23 paired elements + 4 unpaired. **Figure 18.** *E. rosea* (UC51.642, $n = 34$) \times *E. setosa* var. *ciliata* (Moran 7733, $n = 25$). 25 paired + 2 unpaired. **Figure 19.** *E. rosea* (Moran 7815, $n = 34$) \times *E. coccinea* (Moran 7788, $n = 25$). 25 paired elements. **Figure 20.** *E. sp.* ser. *Gibbiflorae* (U2138, $n = 27$) \times *E. rosea* (U1861, $n = 34$). 27 + 4. **Figure 21.** *Pachyphytum hookeri* (Moran 13349, $n = 32$) \times *E. rosea* (U1861, $n = 34$). 32 paired elements. **Figure 22.** *Sedum cuspidatum* (U1263, $n = 34$) \times *E. rosea* (Moran 10068, $n = 34$). 34 paired elements. **Figure 23.** *S. lucidum* (U1462, $n = 34$) \times *E. rosea* (Moran 10098, $n = 34$). 34. **Figure 24.** *E. rosea* (Moran 7815, $n = 34$) \times tetraploid *E. leucotricha* (U1203, $n = 38$). 19 paired elements + 14 unpaired. **Figure 25.** *Graptopetalum fruticosum* (U1398, $n = 31$) \times *E. tencho* (Moran 13754, $n = 51$). 25 + 14. **Figure 26.** *P. hookeri* (Moran 13349, $n = 32$) \times *E. tencho* (Moran 13754, $n = 51$). ca. 28 + 11. **Figure 27.** *E. tencho* (UC58.847, $n = 51$) \times *P. viride* (Moran 10179, $n = 33$). ca. 32 + 5. **Figure 28.** *E. pittieri* (UC57.238, $n = 62$) \times *E. tencho* (UC58.847, $n = 51$). 38 + 2. **Figure 29.** *E. tencho* (U498, $n = 51$) \times *E. coccinea* (Moran 7788, $n = 25$). 25 + 8. **Figure 30.** *E. pittieri* (UC57.238, $n = 62$) \times *E. australis* (UC57.021, $n = 28$). 31 + 11. **Figure 31.** *P. hookeri* (Moran 13349, $n = 32$) \times *E. pittieri* (U2590, $n = 62$) ca. 7 + 78.

ed, and two sets of 25 chromosomes each from *U2665* also pair preferentially with each other, accounting for the 46 pairs observed.

A hybrid between *U2665* and *E. cf. steyermarkii* ($n = 28$), a diploid species of series *Gibbiflorae* from Guatemala (Uhl, 2004), formed about 23–30 paired and 11–32 unpaired elements in 14 cells analyzed at metaphase I. Many chromosomes lagged behind at anaphase I, and one cell at metaphase II had 40 elements on one plate, 38 on the other, and one more not on either plate, accounting for all 79 of the hybrid's chromosomes. Its mature microspores differed greatly in size, and the hybrid must be sterile. All these features are expected in a triploid hybrid.

A hybrid of *U2665* ($n = 50 + 1$) as seed parent with the hairy diploid *E. pulvinata* ($n = 23$) is glabrous but otherwise intermediate in appearance. Meiosis is nearly normal, and six cells at metaphase I had 46 to 49 elements, most of them bivalents, and nearly all of the pollen looks normal. This hybrid is probably fertile, but this was not tested. This cross was expected to yield a triploid hybrid with very irregular meiosis. However, it appears to have resulted from functioning of an unreduced male gamete from *E. pulvinata* that carried 46 chromosomes, representing two sets of 23 chromosomes each. This gamete fused with a female gamete carrying 50 chromosomes from *U2665*. In the hybrid, the 46 chromosomes from *E. pulvinata* form 23 pairs at meiosis, while the 50 chromosomes from *U2665* usually form 25 more.

The most likely interpretation is that *U2665* with $n = 50 + 1$ represents an autotetraploid derived from a diploid with $n = 25$. The similar plants with $n = 51$ possibly evolved from an autotetraploid like *U2665* by the accumulation of mutations and structural rearrangements until its four originally very similar genomes diverged into two kinds. This process is called diploidization, and at meiosis such plants behave more like diploids or allotetraploids.

Whatever the case, the cytological evidence indicates clearly that *E. rosea* with $n = 34$ and *E. tencho* with $n = 51$ are not descended from a common ancestor with $n = 17$. These two species are not nearly as closely related as their vegetative appearance suggests.

Walther (1972) also included *E. pittieri* of Central America in series *Spicatae*, and Kimnach (2003) agrees. At meiosis most cells form 62 pairs very clearly with none of the multivalents that generally characterize autotetraploid species (Fig. 16). In their hybrids the pattern of pairing of their chromosomes also does not conform clearly to that characteristic of autotetraploids in other species of *Echeveria*.

A hybrid of *E. pittieri* as seed parent with autotetraploid *E. secunda* ($n = 32$) looks much more like its pollen parent, as expected if *E. pittieri* were diploid and this hybrid were

triploid. However, most of its chromosomes usually formed pairs at meiosis (Table 1), as expected if both parents were autotetraploid or nearly so. A hybrid between *E. pittieri* and *E. tencho* formed about 44 to 51 paired and 0–6 unpaired elements at meiosis in ten cells that could be analyzed (Table 1, Fig. 28). A hybrid between *E. pittieri* and the diploid Costa Rican *E. australis* ($n = 28$) formed about 31 paired and 11 unpaired elements in the only cell that could be analyzed at metaphase I (Fig. 30), and a hybrid between *E. pittieri* and diploid *Pachyphytum hookeri* ($n = 32$) had less pairing (Fig. 31). All of these hybrids apparently received many chromosomes from *E. pittieri* that can pair with each other, although not all of them do so. *E. pittieri* appears to be an allotetraploid derived by partial diploidization of an autotetraploid ancestor with four similar sets of 31 chromosomes each, but its ancestors are not apparent.

We believe that the evidence from the chromosomes and hybrids shows clearly that the species of series *Spicatae* are not closely related. The series appears to have been based on arbitrary choice of several characters that they happen to share. More study is needed to determine their true relationships.

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Appendix 1. Collections Studied

Echeveria rosea (n = 34)

- Chiapas: Epiphytic on oak, Yola. *R. Alava s. n.* (= UC57.699).
- Chiapas: 12 km toward Ocosingo from San Cristobal de las Casas, 2400 m. *L. McCook & E. Greenwood s. n.* (= Ubl 2884).
- Hidalgo: Puerto Obscuro. *Moran & Kimnach 7813*. Same locality, on rocks. *Ubl 1861*.
- Hidalgo: 1.5 km south of Santa Ana. *Ubl 1862*.
- Hidalgo: woods 3 km east of Zacualtipán. *Moran 10068*.
- Oaxaca: Portillo de San Andrés. *Moran & Kimnach 7758*.
- Oaxaca: El Punto. *Moran & Kimnach 7763*.
- Oaxaca: Portillo de Zeta. *Moran 10098*.
- Oaxaca: 17.4 miles E of Teotitlan on road to Huautla, *Bauml & Kimnach 406*.
- Puebla: near Esperanza. *Ubl 676* (see text).
- Querétaro: between Xilitla and Jalpán, *Baker et al. 6086*.
- San Luis Potosi: 16 km west of Antiguo Morelos. *R. Flores 51* (= UC51.64).
- San Luis Potosi: El Platanito. *Moran & Kimnach 7815*.

Echeveria tencho (n = 51)

- Oaxaca: epiphytic on oak, Cerro Guajinicuil, San-

tiago Guevea, 3000'. *T. MacDougall B201* (= UC58.861).

Same locality, in soil. *T. MacDougall B202* (= UC58.847).

Oaxaca: Agua Zarca. *T. MacDougall B276* (= *Moran 13754*).

Oaxaca: epiphytic, Tenango, Dist. Tehuantepec, 1500 m. *T. MacDougall B11* (= *Ubl 498*) (see text).

Veracruz: Catemaco, 390 m. *T. MacDougall B266* (= *Moran 13277*).

Echeveria tencho (n = 50 + 1).

Oaxaca: road cut 16 km E of Valle Nacional. *J. Bauml & M. Kimnach 486* (= *Ubl 2665*)

Echeveria pittieri (n = 62)

Guatemala: Dept. San Marcos. Rt. Nacional 1 at Km. 246. On rocks at Puente

Nahuatl, 2.2 km. E of plaza at San Pedro Sacatepequez, 2160 m. *Ubl 2590*.

Guatemala: Dept. Baja Vera Paz. Salamá. *E. U. Clover. UC54.1244*.

Guatemala: Dept. Quetzaltenango. Rt. 3 at Km. 15, below Las Nubes, *C. K. Horich*. Epiphytic. *UC57.238*.