

A NEW BASE CHROMOSOME NUMBER AND PHYLOGENY FOR *ERIOPHYLLUM* (ASTERACEAE, HELENIEAE)

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ABSTRACT

Meiotic analysis shows that in *Eriophyllum nevinii* $2n = 19$ II, a new base number for the genus, which now has at least six haploid numbers. The haploid numbers are explainable by either descending basic dysploidy accompanied by dysploid increase and decrease at the polyploid level, or descending basic dysploidy only.

As the dynasties of cytotaxonomy, experimental taxonomy, numerical taxonomy, and chemotaxonomy scroll away on the monitor of systematics, it may seem presumptuous to present this paper during the reign of the current regime, molecular systematics. After all, "Who counts chromosomes these days?" (Kruckeberg 1997, p. 181). But, as Constance (1964) observed, systematics is an unending synthesis. I offer the following in that spirit.

The eriophyllums are a disparate lot, radiate or discoid, from 1 cm to 2 m, in communities as different as seashore, desert, and treeline. A long list of synonyms portrays attempts to delineate taxonomic relationships. Constance (1937) used alpha taxonomic methods to prune a taxonomic thicket into 11 species and 12 varieties. Carlquist (1956) discussed generic limits of *Eriophyllum* and provided cytological and morphological information on it and *Monolopia*, *Pseudobahia*, and *Syntrichopappus*. Johnson's (1978) chemical, cytological, and morphological study of the Eriophyllinae *sensu* Rydberg (1915) included *Lembertia*, the only other genus of the subtribe. Johnson also reviewed the taxonomic history of the Eriophyllinae. Mooring and Johnson (1993) treated, respectively, the six perennial and eight annual species of *Eriophyllum*. Carlquist (1956), Johnson (1978), and Mooring (1986) reported their own and others' chromosome counts for the annual species, namely $n = 4$ (*E. lanosum*), $n = 5$ (*E. wallacei*), and $n = 7$ (*E. ambiguum*, *E. multicaule*, *E. pringlei*, *E. congdonii*, *E. nubigenum*). An $n = 8$ report for *E. pringlei*, given as a new count (Keil and Pinkava 1976), probably represents 7 II plus 2 supernumerary chromosomes. Previous reports for *E. pringlei* were 7 II, 7 II + 1B, and 7 II + 2B (Carlquist 1956; Strother 1976; Johnson 1978). Supernumerary chromosomes are present in some of the other annuals (Strother 1972, 1976; Johnson 1978) and perennials (Mooring 1975, 1994, and unpublished). They

have been a source of error in chromosome counts for other species (Stuessy 1990).

As for the perennials, the widespread and common *E. confertiflorum* var. *confertiflorum* and *E. lanatum* are polyploid complexes in which $n = 8, 16, 24,$ and 32 (Carlquist 1956; Mooring 1975, 1994). Three other perennial taxa seem to exist only as polyploids; *E. latilobum* is tetraploid and *E. jepsonii* and *E. confertiflorum* var. *tanacetiflorum* are octoploids (Carlquist 1956; Mooring 1973). The first two are rare or uncommon (Skinner and Pavlik 1994) and probably originated independently by hybridization between *E. confertiflorum* and *E. lanatum* (Constance 1937; Munz 1959); the latter may have (Mooring 1994). Comparatively few counts have been reported for the remaining two perennials. Carlquist (1956) reported $n = 16$ in three populations of *E. staechadifolium* from Monterey and San Luis Obispo counties and in one population of *E. nevinii* from Santa Catalina Island. Mooring (1973) and Strother (*in* Mooring 1973), however, reported $n = 15$ in eight *E. staechadifolium* populations from Monterey to Humboldt counties, and Keil and Pinkava (1976) found $n = 15$ in a San Luis Obispo County population. The $n = 16$ counts for *E. staechadifolium* seemed to be in error. Was the $n = 16$ counts for *E. nevinii*, a taxon probably derived from *E. staechadifolium* (Constance 1937), also in error?

In this paper, I record a new chromosome number for *Eriophyllum*, discuss the range of haploid chromosome numbers in the genus, and hypothesize a phylogeny based on descending dysploidy, geographic distribution, and habitat considerations.

MATERIALS AND METHODS

Eriophyllum nevinii, rare and threatened (Skinner and Pavlik 1994), is endemic to the southern Channel Islands of California. Obtaining buds from botanical gardens was more feasible than getting them from natural populations. Unfortunately, my 1992 and 1994 collections, from the Santa Barbara Botanic Garden, turned out to be from plants of unknown provenance, believed to be members of one clone. Plants derived from cuttings whose source was known became available in 1995, at the University of California, Berkeley, Botanic Garden, and the Santa Barbara Botanic Garden, from, respectively, Middle Ranch Canyon and Mesquite Cove Canyon, San Clemente Island. Fruits from Santa Barbara Island, provided by the Santa Barbara Botanic Garden, yielded another plant. Capitula from eight plants of unknown provenance, and from five of known provenance were fixed in 1:3 acetic ethanol. Microspores were squashed in acetocarmine and examined with a phase-contrast microscope. Meiotic stages suitable for counts were uncommon. Observation of at least 10 clear diakinesis, first metaphase, or

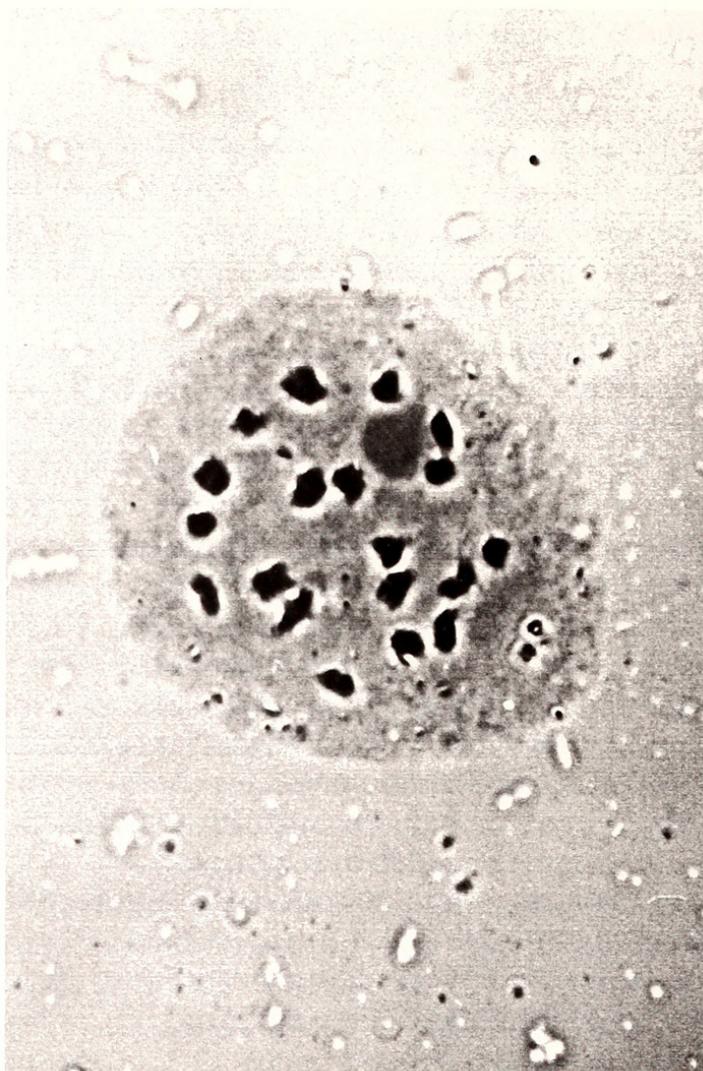


FIG. 1. Photograph of diakinesis in a microsporocyte of *Eriophyllum nevinii*, $2n = 19 \text{ II}$.

anaphase cells from each of nine plants was accompanied by sketches, camera lucida drawings, and a photomicrograph. Voucher specimens are deposited in SBBG (*Junak* 5243, 5244, 5809, 5810), JEPS (87556), and SACL (*Mooring* 3934, 3993).

RESULTS AND DISCUSSION

The microsporocytes taken in 1992 from unprovenanced plants at the Santa Barbara Botanic Garden were difficult to analyze. The chromosomes were sticky, irregularly condensed, and often overlapping. Three plants yielded counts varying from 17 to 19 II. The clearest cells suggested 18 II. Examination of the 1994 material (same site, different plants) gave 17–19 II for one plant, and 18 II + 1 I for the other. The 1995 material derived from Middle Ranch Canyon, San Clemente Island, however, showed 19 II (Fig. 1), as did 1996 material from Mesquite Cove Canyon, San Clemente Is-

land, and 1997 material from Santa Barbara Island. Reviewing the camera lucida drawings and sketches of the unprovenanced material that gave the 18 II counts suggests that what was interpreted as one bivalent was probably two greatly and irregularly condensed bivalents connected by a thread.

The distinct difference in chromosome number between *E. nevinii* and its presumed progenitor, *E. staechadifolium* (Constance 1937, p. 73), was adumbrated by Constance's (1937, p. 114) comment that *E. nevinii* is "beautifully distinct".

Possibly *E. staechadifolium* and *E. nevinii* are tetraploid derivatives with undiscovered diploid populations. If diploid populations with known base numbers do not exist, at least six haploid numbers occur in *Eriophyllum* ($n = 4, 5, 7, 8, 15, 19$). The rare annual species *E. mohavense* (Skinner and Pavlik 1994) is still uncounted.

At this point I introduce what seems to me to be a useful concept to express the amount of variation in base chromosome numbers in taxa of similar size, the "base chromosome number index", obtained by dividing the number of species per genus by the number of haploid chromosome numbers known. The base chromosome number index (hereafter BCNI) for *Eriophyllum* is $14/6$, or 2.3, i.e., one base number for every 2.3 species. No other comparable-sized genus in the Helenieae appears to have this much variation in base chromosome numbers. *Lasthenia*, with 17 species and five base numbers (Ornduff 1966), is the nearest contender, with a BCNI of $3.4 (17/5)$, one base number for every 3.4 species. Clearly, taxa with more than one base number and a sufficiently small number of species will have low BCNIs. Among the Eriophyllinae, for example, the BCNIs for *Monolopia* (3 species), *Pseudobahia* (3 species), and *Syntrichopappus* (2 species) are, respectively, 1.3, 1.0, and 1.0. The range of base chromosome numbers ($x = 4, 5, 7, 8, 15, 19$) in *Eriophyllum* suggests extensive chromosomal repatterning, a polyphyletic origin, or both. Ongoing studies by Bruce Baldwin (e.g., Baldwin and Wessa 1997) will no doubt clarify matters.

Constance (1937, pp. 72–73), before chromosome numbers were reported in *Eriophyllum*, hypothesized that the perennial *E. lanatum* ($x = 8$) most nearly represented the primitive stock of the genus. His prescient representation of phylogenetic relationships (1937, p. 73) parallels a *descending* series in the annual species: *E. nubigenum* ($n = 7$) to the other $n = 7$ species *E. congdonii*, *E. ambiguum*, *E. multicaule*, and *E. pringlei*, and to an ancestor that produced *E. wallacei* ($n = 5$) and *E. lanosum* ($n = 4$). Or, *E. multicaule* and *E. pringlei* might have been derived from the perennial and $x = 8$ *E. confertiflorum*. On the other hand, in the perennial species Constance's (1937, p. 73) *E. lanatum*–*E. staechadifolium*–*E. nevinii* phylogeny parallels an *ascending* $n = 8$ – 15 – 19 series, possibly resulting from polyploidy followed by dysploid decrease ("polyploid drop")

and increase at the polyploid level (Grant 1981, pp. 358–364, as aneuploidy rather than dysploidy).

A descending dysploidy phylogeny with *E. nevinii* rather than *E. lanatum* as the most primitive stock is also possible. Descending basic dysploidy occurs more frequently than ascending dysploidy and is known in more than 20 groups (Grant 1981). In fact, Grant (1981, p. 358) cited an 8–7–()–4–3 sequence (now 8–7–()–5–4–3) for haploid numbers in *Eriophyllum* and *Pseudobahia*, the symbol “()” representing missing numbers in the series. Haploid chromosome number, geographic distribution, habitat considerations, and, in part, crossability relationships suggest that *E. nevinii* might represent the most primitive stock, and that reduction in chromosome number has accompanied migration northward and eastward, from maritime to desert environments, and from perennial to annual habit (Tables 1, 2; Fig. 2).

Attempts to cross *E. nevinii* ($n = 19$) and *E. staechadifolium* ($n = 15$) have been unsuccessful, as have been all but one heteroploid cross in my *Eriophyllum* studies (Table 2). Attempts to cross *E. staechadifolium* and *E. confertiflorum* var. *confertiflorum* reciprocally have not yet been made, but pollinating *E. staechadifolium* with pollen from tetraploid *E. lanatum* ($n = 16$) yielded only selfs. Natural, interspecific hybrids have not been reported for these species. Clearly, no evidence exists for a hybridity connection between the maritime and mainly inland perennial species.

Eriophyllum confertiflorum var. *confertiflorum* and *E. lanatum* (both $n = 8$) bridge the chromosome number, distribution, and habitat gap between the maritime perennial species *E. nevinii* ($n = 19$) and *E. staechadifolium* ($n = 15$), on the one hand, and the annual species ($n = 7, 5, \text{ or } 4$) of mostly interior plant communities on the other. Both *E. confertiflorum* var. *confertiflorum* and *E. lanatum* are polyploid complexes with a nonrandom distribution of diploid and tetraploid populations (Mooring 1975, 1994). Eighteen of the 23 *E. confertiflorum* var. *confertiflorum* populations sampled from Los Angeles County southward were diploid, suggesting that the species migrated from southwestern North America (Mooring 1994). Twenty-five of the 26 southernmost California *E. lanatum* populations are diploid (Mooring 1975 and unpublished), likewise supporting a southern origin for that taxon. The diploid populations of each complex occur in coastal communities and also in interior sagebrush and desert scrub communities (Table 1). Unfortunately, although chromosome numbers are known from about 300 populations of *E. lanatum* (Mooring 1975, 1986) and 130 of *E. confertiflorum* var. *confertiflorum* (Mooring 1994), comparatively few have been reported for four of the five annual species, *E. ambiguum* (9), *E. multicaule* (3), *E. pringlei* (9), *E. wallacei* (29), and *E. lanosum* (8) (see John-

TABLE 1. HAPLOID CHROMOSOME NUMBERS IN *ERIOPHYLLUM*. Polyploid species are not listed. Names of plant communities are taken from Munz (1959).

Species	x	Range	Plant community
Perennials			
<i>E. nevinii</i>	19	s. California	Coastal Sage Scrub
<i>E. staechadifolium</i>	15	s. California to Oregon	Coastal Sage Scrub, Coastal Strand, N. Coastal Scrub
<i>E. confertiflorum</i>	8	Baja California, California	Coastal Sage Scrub to Desert Scrub ecotones
var. <i>confertiflorum</i>	8	California to British Columbia, Utah, Wyoming	Northern Coastal Scrub to Sagebrush Scrub
<i>E. lanatum</i>	8		
Annuals			
<i>E. congdonii</i>	7	Mariposa Co., California	Foothill Woodland, Conifer Forest
<i>E. nubigenum</i>	7	Mariposa Co., California	Conifer Forest
<i>E. multicaule</i>	7	central to s. California	Coastal Sage Scrub, Chaparral, Foothill Woodland
<i>E. ambiguum</i>	7	s. California, Nevada	Foothill, Pinyon-Juniper, and Joshua-Tree Woodlands, Creosote Bush Scrub
<i>E. pringlei</i>	7	s. California, Nevada, Arizona	Chaparral, Sagebrush Scrub, Joshua-Tree Woodland, Creosote Bush Scrub
<i>E. mohavense</i>	?	s. California	Creosote Bush Scrub
<i>E. wallacei</i>	5	Baja California to central California, Nevada, Utah	Chaparral, Joshua-Tree Woodland, Creosote Bush Scrub
<i>E. lanosum</i>	4	northwest Mexico, s. California, Arizona, Nevada, Utah	Creosote Bush Scrub

TABLE 2. SUMMARY OF ARTIFICIAL HYBRIDIZATION RESULTS IN *ERIOPHYLLUM*. All are at the diploid level, unless otherwise stated. Most crosses involve one or a few plants from one population of each species.

<i>E. nevinii</i> ($n = 19$) \times <i>E. staechadifolium</i> ($n = 15$)	PERENNIALS, NO HYBRIDS FORMED
<i>E. staechadifolium</i> ($n = 15$) \times tetraploid <i>E. lanatum</i> ($n = 16$)	
<i>E. lanatum</i> ($n = 8$) \times <i>E. confertiflorum</i> ($n = 8$) many combinations	PERENNIALS, VIGOROUS HYBRIDS, FERTILITY REDUCED
<i>E. lanatum</i> ($n = 8$) \times <i>E. ambiguum</i> ($n = 7$)	PERENNIALS \times ANNUALS, NO HYBRIDS FORMED
<i>E. lanatum</i> ($n = 8$) \times <i>E. congonii</i> ($n = 7$)	PERENNIALS \times ANNUALS, STERILE HYBRIDS FORMED
<i>E. ambiguum</i> ($n = 7$) \times <i>E. wallacei</i> ($n = 5$) and <i>E. lanosum</i> ($n = 4$)	ANNUALS \times ANNUALS, HETEROPLOIDS, NO HYBRIDS FORMED
<i>E. congonii</i> ($n = 7$) \times <i>E. wallacei</i> ($n = 5$) and <i>E. lanosum</i> ($n = 4$)	
<i>E. multicaule</i> ($n = 7$) \times <i>E. wallacei</i> ($n = 5$) and <i>E. lanosum</i> ($n = 4$)	
<i>E. nubigenum</i> ($n = 7$) \times <i>E. wallacei</i> ($n = 5$) and <i>E. lanosum</i> ($n = 4$)	
<i>E. pringlei</i> ($n = 7$) \times <i>E. wallacei</i> ($n = 5$) and <i>E. lanosum</i> ($n = 4$)	
<i>E. wallacei</i> ($n = 5$) \times <i>E. lanosum</i> ($n = 4$)	ANNUALS \times ANNUALS, HOMOPLOIDS, NO HYBRIDS FORMED
<i>E. congonii</i> ($n = 7$) \times <i>E. pringlei</i> ($n = 7$)	
<i>E. multicaule</i> ($n = 7$) \times <i>E. nubigenum</i> ($n = 7$)	
<i>E. nubigenum</i> ($n = 7$) \times <i>E. pringlei</i> ($n = 7$)	ANNUALS \times ANNUALS, STERILE HYBRIDS FORMED
<i>E. ambiguum</i> ($n = 7$) \times <i>E. congonii</i> ($n = 7$), <i>E. multicaule</i> ($n = 7$), <i>E. nubigenum</i> ($n = 7$), <i>E. pringlei</i> ($n = 7$)	
<i>E. congonii</i> ($n = 7$) \times <i>E. multicaule</i> ($n = 7$)	
<i>E. multicaule</i> ($n = 7$) \times <i>E. pringlei</i> ($n = 7$)	ANNUALS \times ANNUALS, VIGOROUS, FERTILE HYBRIDS FORMED
<i>E. congonii</i> ($n = 7$) \times <i>E. nubigenum</i> ($n = 7$)	

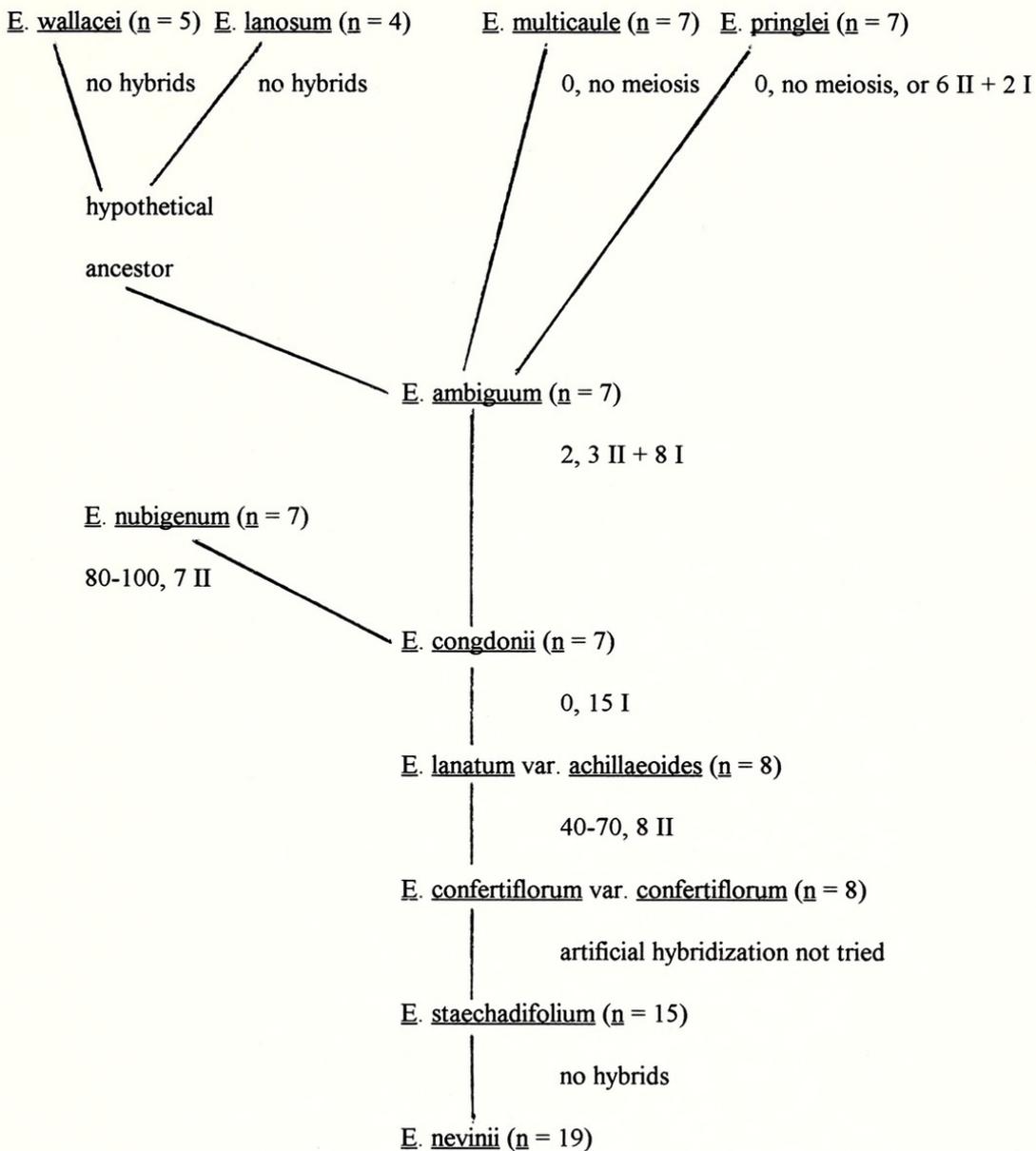


FIG. 2. Hypothetical phylogeny of *Eriophyllum*, showing percent stainable pollen and maximum meiotic configuration of artificial F_1 hybrids between the species.

son 1978). More counts would be desirable, especially from the possibly extinct *E. mohavense*.

Putative natural hybrids between *E. confertiflorum* and four varieties of *E. lanatum* have been observed (Constance 1937; Thomas 1961; Mooring 1994). At the diploid level their artificial F_1 hybrids are vigorous and almost always form 8 II at diakinesis or first metaphase, but pollen stainability averages less than 40% (Mooring 1994 and unpublished). If they did not originate from a common ancestor, morphology and geography suggest that *E. lanatum* originated from an *E. confertiflorum* var. *confertiflorum* plexus.

The annual species *E. congdonii* ($n = 7$) is probably nearest to *E. lanatum* ($n = 8$). Superficially, it closely resembles *E. lanatum*

var. *grandiflorum*. Artificial hybridizations between either *E. lanatum* var. *grandiflorum* or *E. lanatum* var. *achillaeoides* and *E. congdonii* produced vigorous F_1 hybrids with pollen stainabilities of 1% or less and meiotic configurations of 15 I (Mooring 1991). Artificial hybridization between *Eriophyllum congdonii* and the equally rare (Skinner and Pavlik 1994) *E. nubigenum* produced vigorous and fertile hybrids (Mooring 1991). On the other hand, *E. nubigenum* \times *E. lanatum* var. *grandiflorum* and *E. nubigenum* \times *E. multicaule* crosses yielded only seeds of the former (Table 2) casting doubt on Constance's (1937) hypothesis that *E. nubigenum* was a link between *E. lanatum* and *E. multicaule*.

Morphology and artificial hybridizations (Table 2, Fig. 2) suggest that *E. ambiguum* is the annual species most closely related to *E. congdonii*. They are difficult to tell apart macroscopically when grown side-by-side in the greenhouse. Hybrids constituted about 25% of one progeny, pollen stainability averaged 2%, and the maximum meiotic configuration was 3 II + 8 I (Fig. 2). *Eriophyllum ambiguum* links, in this hypothetical phylogeny (Fig. 2), the other annual species to *E. congdonii*. It forms sterile hybrids with the $n = 7$ species *E. multicaule* and *E. pringlei*, having no microspores in one cross, and forming from 2 II + 10 I to 6 II + 2 I in another (Fig. 2). Attempts to cross *E. ambiguum* with either *E. wallacei* ($n = 5$) or *E. lanosum* ($n = 4$) have been unsuccessful. Like Constance (1937), I hypothesize at least one hypothetical ancestor between these species and *E. ambiguum*, although on morphological grounds it is tempting to contemplate *E. wallacei* as more directly derived from *E. ambiguum*. Table 2 shows the results of other crosses not mentioned above.

The pattern of lower chromosome numbers in the annual eriophyllums and higher ones in the perennials fits Stebbins's (1950, pp. 167–170) discussion of chromosomal mechanisms and genetic systems. Lower chromosome numbers tend to accompany the annual habit, higher ones the perennial mode, thus helping balance fitness and evolutionary flexibility. Mode of pollination is also involved. Stebbins (1950, p. 168) observed that a "large proportion of annual species are predominantly self-pollinated." The annuals *E. nubigenum* and *E. congdonii* are partly self-compatible (Mooring 1991), and that seems to be true of the other annual species of the genus (Mooring unpublished). Contrariwise, the perennials *E. confertiflorum*, *E. jepsonii*, *E. latilobum*, and *E. lanatum* are almost completely self-incompatible (Mooring unpublished). The perennials and the $n = 7$ annual eriophyllums live in more mesic habitats than the $n = 5$ or $n = 4$ annual species (Table 1). In these environmentally more open communities, low chromosome number and partial self-compatibility would favor fitness at the expense of flexibility.

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