

# PHYLOGENETIC RELATIONSHIPS OF CERTAIN RACES OF *EUOENOTHERA* FROM MEXICO AND GUATEMALA<sup>1</sup>

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## INTRODUCTION

*Oenothera* has long enjoyed biological fame for its unconventional cytogenetic behavior.<sup>2</sup> In recent years these cytogenetic peculiarities have been effectively utilized in determining phylogenetic relationships in the North American section of the subgenus *Euoenothera* (Cleland, 1935, 1937, 1940, 1949). The present paper is a report of similar phylogenetic studies on races of *Euoenothera* from Central America and Mexico. These races, like the California forms, lack cytogenetic specialization. Although similar to the California races phenotypically, they differ sufficiently to be assigned to a distinct species by Munz (1949). The question therefore arises as to whether this group is to be considered closer to the ancestral line of the North American euoenotheras or whether the California group is more primitive. A cytogenetic analysis of the races from Mexico and Guatemala should throw light upon this problem.

The material from Guatemala was studied for another reason also. It has hitherto been difficult to obtain crosses between the North American euoenotheras and the South American forms. It was hoped that races from Central America might cross readily with both North and South American races and hence serve as bridging forms, which would make it possible to bring all of the euoenotheras into

a single cytogenetic system. The Guatemalan material, however, does not cross readily with South American euoenotheras, although it crosses readily with those from North America. Its affinities seem to be definitely North American, and its value as a bridging form is questionable. Further discussion of this phase of the study, therefore, will be omitted from the present paper.

## MATERIALS AND METHODS

The new races analyzed in this study are listed in table I. These were hybridized with a series of "standard" races (table II) whose complexes had previously been analyzed genetically and cytologically. Each hybrid combination was identified phenotypically and its chromosome configuration determined. From these configurations the segmental arrangements of the new complexes were worked out. For further information regarding the standard races see Cleland, 1935, 1937; Cleland and Hammond, 1950; Geckler, 1950; Preer, 1950.

The race *Guatemala* actually represents two collections from Guatemala, one from Guatemala City, the other from Chichicastenango. These two collections proved to be phenotypically and segmentally indistinguishable. For this reason, only the strain from Guatemala City, which we have named *Guatemala*, has been used in the present study.

All cytological material was prepared according to the schedule described by Hecht, 1950. Chromosome configurations were determined from pollen mother cells in late diakinesis or metaphase I. Wherever possible, determinations were obtained from at least two plants of each complex combination.

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<sup>2</sup> For a review of *Oenothera* cytogenetics see Cleland, 1936.

TABLE I. *New races included in the present study*

Race	Source	Collector	Year	Chromosome configuration
Chapultepec	Dist. Fed., Mexico	P. A. Munz	1937	7 pairs
Guatemala	Guatemala City, Guatemala	P. Weatherwax	1945	7 pairs
Texmelucan	Puebla, Mexico	P. A. Munz	1937	7 pairs
Toluca	Mexico, Mexico	P. A. Munz	1937	7 pairs
Zimapan	Hidalgo, Mexico	P. A. Munz	1937	7 pairs

## DESCRIPTION OF NEW RACES

1. *Characters common to all new races:*

*Leaves* of moderate size (largest cauline leaves 8.5–19.5 cm. long, 2–3 cm. wide), light green with a grayish cast, elliptic-lanceolate, acute; surface smooth to very slightly crinkled, strongly wavy; margins entire to obscurely toothed; marginal hairs appressed; surface hairs moderately numerous, fairly short to medium in length, closely appressed; midrib white; pulvinus green.

*Stems.* Papillae usually absent or indistinct; a strong, felty pubescence.

*Habit.* Central shoot usually well developed with numerous lateral branches which often reach the same height as the central shoot; no rosette formation when grown in central Indiana.

*Bracts* moderately to strongly flared, green.

*Buds.* Cone 2.2–3.5 cm., hypanthium 2.3–3.2 cm., ovary 1–1.5 cm.; cone somewhat angular, tapered, 4–6 mm. thick at base, thick skinned, yellow green to red

TABLE II. *Segmental arrangements of previously determined complexes which are involved in the present analysis*

Complex	Race	Formula for segmental arrangement						
$\alpha$ <i>Birch Tree 1</i>	<i>Birch Tree 1</i>	1·2	3·4	5·14	7·10	9·8	11·12	13·6
$\beta$ <i>Birch Tree 1</i>	<i>Birch Tree 1</i>	1·4	3·13	5·7	8·12	9·10	11·6	2·14
$\alpha$ <i>Birch Tree 3</i>	<i>Birch Tree 3</i>	1·5	3·13	2·6	7·12	9·14	11·10	4·8
$\beta$ <i>Birch Tree 3</i>	<i>Birch Tree 3</i>	1·4	3·2	5·11	7·10	9·6	8·14	13·12
<sup>b</sup> <i>blandina</i> *	<i>blandina</i>	1·2	3·4	5·6	7·10	9·14	11·12	13·8
$\alpha$ <i>Camas</i>	<i>Camas</i>	1·9	3·5	4·6	7·10	2·8	11·14	13·12
$\beta$ <i>Camas</i>	<i>Camas</i>	1·4	3·2	5·10	7·14	9·8	11·12	13·6
<i>curtans</i>	<i>cockerelli</i>	1·7	3·4	5·8	2·10	9·11	6·12	13·14
<i>elongans</i>	<i>cockerelli</i>	1·4	3·2	5·10	7·6	9·14	11·12	13·8
<i>excellens</i>	<i>chicaginis</i>	1·2	3·4	5·6	7·10	9·8	11·12	13·14
<i>flavens</i>	<i>suaveolens</i>	1·4	3·2	5·6	7·8	9·10	11·12	13·14
<sup>b</sup> <i>franciscana</i> Shull	<i>franciscana</i> Shull	1·2	3·4	5·6	7·8	9·10	11·12	13·14
<i>gaudens</i>	<i>r-lamarckiana</i>	1·2	3·12	5·6	7·11	9·4	8·14	13·10
<sup>b</sup> <i>hookeri</i> de V.	<i>hookeri</i> de V.	1·2	3·4	5·6	7·8	9·10	11·12	13·14
$\alpha$ <i>Iowa 2</i>	<i>Iowa 2</i>	1·2	3·14	5·8	7·11	9·6	10·12	13·4
$\beta$ <i>Iowa 2</i>	<i>Iowa 2</i>	1·4	3·2	5·10	7·6	9·8	11·13	12·14
$\alpha$ <i>Iowa 6</i>	<i>Iowa 6</i>	1·2	3·13	5·12	7·10	9·6	11·8	4·14
$\beta$ <i>Iowa 6</i>	<i>Iowa 6</i>	1·4	3·2	5·7	6·10	9·14	11·12	13·8
<sup>b</sup> <i>Johansen</i>	<i>Johansen</i>	1·2	3·4	5·6	7·10	9·8	11·12	13·14
<i>jugens</i>	<i>shulliana</i>	1·6	3·2	5·14	7·13	9·8	11·12	4·10
<i>maculans</i>	<i>shulliana</i>	1·2	3·8	5·6	7·10	9·12	11·13	4·14
<i>neo-acuens</i>	<i>grandiflora</i> de V.	1·13	3·2	5·6	7·10	9·8	11·12	4·14
$\alpha$ <i>Paducah</i>	<i>Paducah</i>	1·2	3·4	5·14	7·10	9·8	11·12	13·6
$\beta$ <i>Paducah</i>	<i>Paducah</i>	1·14	3·2	5·9	7·8	6·12	11·10	13·4
<i>punctulans</i>	<i>chicaginis</i>	1·4	3·9	5·2	7·8	6·12	11·10	13·14
<i>truncans</i>	<i>grandiflora</i> de V.	1·13	3·7	5·2	4·6	9·14	11·10	8·12
<i>velans</i>	<i>r-lamarckiana</i>	1·2	3·4	5·8	7·6	9·10	11·12	13·14

\* The superscript "h" (haplo-) indicates that the complex occurs in duplicate in a homozygous race.

with numerous, long, closely appressed hairs; sepal tips 5–6 mm. long, appressed; hypanthium yellow green; ovary gray green; stamens do not reach stigma; petals extend to, or beyond, stigma.

*Petals* fairly large, 2.5–3.5 cm. wide, 2–3 cm. long.

*Flowers* 4.5–5.5 cm. in diameter.

*Fruit* thick at base.

*Height* as grown, 98–132 cm.

## II. Characters distinguishing individual races:

*Chapultepec*: Stems with very deep red basal color which masks tip and papillae color; papillae, if present, indistinct; bud cone red; fruit with longitudinal red bands at corners.

*Guatemala*: Leaves smaller than in other races in this collection (typical lower cauline leaf  $8.5 \times 2$  cm.); stems lacking basal color; tips below bracts very slightly red late in the season; stem hairs lacking except for the strong, felty pubescence; papillae absent; habit distinctive in that the lowest lateral branches arise from the central shoot several inches above the ground. Cone shorter and thinner than in other races here included, yellow green; stigma characteristically protrudes from the bud before the flower opens; petals and flowers smaller than in other races of this collection.

*Texmelucan*: Stems with a moderate basal color; tips below bracts green; bud cone reddened along sutures.

*Toluca*: Stems with a slight to moderate basal color; tips green, bud cone yellow green.

*Zimapan*: Stems with a strong red basal color, but less pronounced than in *Chapultepec*; tips red, papillae red; bud cone red; ovary with red papillae.

## HYBRIDIZATION

The crosses obtained by hybridizing Guatemalan and Mexican races with the standard races are listed in table III. In general such crosses were highly success-

ful and ample seed was obtained. With very few exceptions germination was uniformly high and the hybrid seedlings were vigorous. The complex combinations <sup>h</sup>*Guatemala*·*curvans* (*Guatemala* × *muricata*), <sup>h</sup>*Chapultepec*·*curvans* (*Chapultepec* × *muricata*) and <sup>h</sup>*Guatemala*·*maculans* (*Guatemala* × *shulliana*) failed to survive, however, because of plastid difficulties. In addition, the following complex combinations showed varying degrees of chlorosis: *flavens*·<sup>h</sup>*Texmelucan*, *aCamas*·<sup>h</sup>*Texmelucan*, *gaudens*·<sup>h</sup>*Texmelucan*, *flavens*·<sup>h</sup>*Toluca*, *gaudens*·<sup>h</sup>*Toluca*, and <sup>h</sup>*Chapultepec*·*aPaducah*; these combinations reached maturity, however, in spite of chlorosis."

No attempt was made to carry out a genetic analysis of specific characters shown by these races. Since all the races are homozygous (with respect to chromosomal end arrangement), the phenotypic characters produced by each complex are those reported in the description of the race in which it occurs. The race *Guatemala*, it will be noted, lacks red pigmentation other than a slight tip color when the plants are mature. Evidence from certain hybrids with *Guatemala* indicates, however, that <sup>h</sup>*Guatemala* carries a factor for red pigmentation which is ordinarily suppressed in the race itself and in most hybrid combinations. In a few cases, e.g., <sup>h</sup>*Guatemala*·<sup>h</sup>*Alabama*, red papillae, basal color, and cones are shown, even though <sup>h</sup>*Alabama* lacks a factor for red pigmentation. The latter complex is presumed to carry a gene preventing the action of the suppressor of color which appears to be present in <sup>h</sup>*Guatemala*. Additional crosses are being made to analyze the situation more fully.

## CYTOLOGICAL ANALYSIS

To illustrate the manner in which the segmental arrangement of a complex can be derived, the reasoning used to determine the segmental arrangement of <sup>h</sup>*Guatemala* will be given. The segmental arrangements of the other complexes (table

TABLE III. Newly determined chromosome configurations

Cross	Complex combination	Chromosome configuration
<i>Birch Tree 3</i> × <i>Texmelucan blandina</i> ×	$\alpha$ <i>Birch Tree 3</i> · $^b$ <i>Texmelucan blandina</i> · $^b$ <i>Texmelucan blandina</i> · $^b$ <i>Toluca</i>	⊙ <sup>1</sup> 8, ⊙ 4, 1 pair ⊙ 4, 5 pairs ⊙ 4, 5 pairs
× <i>Zimapan</i>	$^b$ <i>blandina</i> · $^b$ <i>Zimapan</i>	⊙ 4, 5 pairs
<i>Camas</i> × <i>Guatemala</i>	$\alpha$ <i>Camas</i> · $^b$ <i>Guatemala</i>	⊙ 10, ⊙ 4
<i>Chapultepec</i> × <i>Birch Tree 1</i> ×	$^b$ <i>Chapultepec</i> · $\alpha$ <i>Birch Tree 1</i>	⊙ 6, ⊙ 4, 2 pairs
× <i>Birch Tree 3</i>	$^b$ <i>Chapultepec</i> · $\beta$ <i>Birch Tree 1</i> $^b$ <i>Chapultepec</i> · $\alpha$ <i>Birch Tree 3</i> $^b$ <i>Chapultepec</i> · $\beta$ <i>Birch Tree 3</i>	⊙ 12, 1 pair ⊙ 8, ⊙ 4, 1 pair ⊙ 8, 3 pairs
× <i>blandina</i>	$^b$ <i>Chapultepec</i> · $^b$ <i>blandina</i>	⊙ 4, 5 pairs
× <i>Camas</i>	$^b$ <i>Chapultepec</i> · $\beta$ <i>Camas</i>	⊙ 8, 3 pairs
× <i>chicaginisensis</i>	$^b$ <i>Chapultepec</i> · <i>punctulans</i>	⊙ 12, 1 pair
× <i>cockerelli</i>	$^b$ <i>Chapultepec</i> · <i>elongans</i>	⊙ 4, 5 pairs
× <i>franciscana</i> S.	$^b$ <i>Chapultepec</i> · $^b$ <i>franciscana</i> Shull	⊙ 6, ⊙ 4, 2 pairs
× <i>grandiflora</i>	$^b$ <i>Chapultepec</i> · <i>neo-acuens</i> $^b$ <i>Chapultepec</i> · <i>truncans</i>	⊙ 6, 4 pairs ⊙ 12, 1 pair
× <i>Johansen</i>	$^b$ <i>Chapultepec</i> · $^b$ <i>Johansen</i>	⊙ 4, ⊙ 4, 3 pairs
× <i>Paducah</i>	$^b$ <i>Chapultepec</i> · $\alpha$ <i>Paducah</i>	⊙ 6, ⊙ 4, 2 pairs
<i>chicaginisensis</i> × <i>Zimapan</i>	<i>excellens</i> · $^b$ <i>Zimapan</i>	⊙ 4, ⊙ 4, 3 pairs
<i>cockerelli</i> × <i>Texmelucan</i>	<i>curtans</i> · $^b$ <i>Texmelucan</i>	⊙ 8, ⊙ 6
× <i>Zimapan</i>	<i>curtans</i> · $^b$ <i>Zimapan</i> <i>elongans</i> · $^b$ <i>Zimapan</i>	⊙ 8, ⊙ 6 ⊙ 4, 5 pairs
<i>franciscana</i> Sh. × <i>Texmelucan</i>	$^b$ <i>franciscana</i> Sh. · $^b$ <i>Texmelucan</i>	⊙ 6, ⊙ 4, 2 pairs
× <i>Zimapan</i>	$^b$ <i>franciscana</i> Sh. · $^b$ <i>Zimapan</i>	⊙ 6, ⊙ 4, 2 pairs
<i>grandiflora</i> × <i>Zimapan</i>	<i>neo-acuens</i> · $^b$ <i>Zimapan</i> <i>truncans</i> · $^b$ <i>Zimapan</i>	⊙ 6, 4 pairs ⊙ 12, 1 pair
<i>Guatemala</i> × <i>Camas</i>	$^b$ <i>Guatemala</i> · $\beta$ <i>Camas</i>	⊙ 12, 1 pair
× <i>Chapultepec</i>	$^b$ <i>Guatemala</i> · $^b$ <i>Chapultepec</i>	⊙ 6, ⊙ 6, 1 pair
× <i>cockerelli</i>	$^b$ <i>Guatemala</i> · <i>elongans</i>	⊙ 12, 1 pair
× <i>grandiflora</i>	$^b$ <i>Guatemala</i> · <i>neo-acuens</i> $^b$ <i>Guatemala</i> · <i>truncans</i>	⊙ 8, ⊙ 4, 1 pair ⊙ 8, ⊙ 6
× <i>hookeri</i>	$^b$ <i>Guatemala</i> · $^b$ <i>hookeri</i>	⊙ 8, 3 pairs
× <i>Iowa 2</i>	$^b$ <i>Guatemala</i> · $\beta$ <i>Iowa 2</i>	⊙ 10, ⊙ 4
× <i>Iowa 6</i>	$^b$ <i>Guatemala</i> · $\beta$ <i>Iowa 6</i>	⊙ 12, 1 pair
× <i>shulliana</i>	$^b$ <i>Guatemala</i> · <i>jugens</i>	⊙ 12, 1 pair
× <i>Texmelucan</i>	$^b$ <i>Guatemala</i> · $^b$ <i>Texmelucan</i>	⊙ 6, ⊙ 6, 1 pair
× <i>Toluca</i>	$^b$ <i>Guatemala</i> · $^b$ <i>Toluca</i>	⊙ 6, ⊙ 6, 1 pair
× <i>Zimapan</i>	$^b$ <i>Guatemala</i> · $^b$ <i>Zimapan</i>	⊙ 6, ⊙ 6, 1 pair
<i>Iowa 2</i> × <i>Guatemala</i>	$\alpha$ <i>Iowa 2</i> · $^b$ <i>Guatemala</i>	⊙ 8, ⊙ 4, 1 pair
<i>Johansen</i> × <i>Guatemala</i>	$^b$ <i>Johansen</i> · $^b$ <i>Guatemala</i>	⊙ 4, ⊙ 4, 3 pairs
× <i>Texmelucan</i>	$^b$ <i>Johansen</i> · $^b$ <i>Texmelucan</i>	⊙ 4, ⊙ 4, 3 pairs
× <i>Zimapan</i>	$^b$ <i>Johansen</i> · $^b$ <i>Zimapan</i>	⊙ 4, ⊙ 4, 3 pairs
<i>r-lamarckiana</i> × <i>Texmelucan</i>	<i>gaudens</i> · $^b$ <i>Texmelucan</i> <i>velans</i> · $^b$ <i>Texmelucan</i>	⊙ 12, 1 pair ⊙ 8, ⊙ 4, 1 pair
× <i>Zimapan</i>	<i>gaudens</i> · $^b$ <i>Zimapan</i>	⊙ 12, 1 pair
<i>suaveolens</i> × <i>Texmelucan</i>	<i>flavens</i> · $^b$ <i>Texmelucan</i>	⊙ 6, 4 pairs
× <i>Toluca</i>	<i>flavens</i> · $^b$ <i>Toluca</i>	⊙ 6, 4 pairs
<i>Texmelucan</i> × <i>chicaginisensis</i>	$^b$ <i>Texmelucan</i> · <i>punctulans</i>	⊙ 12, 1 pair
× <i>hookeri</i>	$^b$ <i>Texmelucan</i> · $^b$ <i>hookeri</i>	⊙ 6, ⊙ 4, 2 pairs
<i>Toluca</i> × <i>Chapultepec</i>	$^b$ <i>Toluca</i> · $^b$ <i>Chapultepec</i>	7 pairs
× <i>chicaginisensis</i>	$^b$ <i>Toluca</i> · <i>punctulans</i>	⊙ 12, 1 pair
× <i>Guatemala</i>	$^b$ <i>Toluca</i> · $^b$ <i>Guatemala</i>	⊙ 6, ⊙ 6, 1 pair
× <i>hookeri</i>	$^b$ <i>Toluca</i> · $^b$ <i>hookeri</i>	⊙ 6, ⊙ 4, 2 pairs
<i>Zimapan</i> × <i>Camas</i>	$^b$ <i>Zimapan</i> · $\beta$ <i>Camas</i>	⊙ 8, 3 pairs
× <i>Paducah</i>	$^b$ <i>Zimapan</i> · $\beta$ <i>Paducah</i>	⊙ 12, 1 pair

<sup>1</sup> The symbol "⊙" means "a circle of"; thus, for example, "⊙ 14" means a circle of fourteen chromosomes.

TABLE IV. Segmental arrangements of complexes in euoenotheras occurring in Mexico and Guatemala

Complex	Segmental arrangement							Designation
<sup>b</sup> Guatemala	1·2	3·10	5·9	7·4	6·8	11·12	13·14	G
<sup>b</sup> Chapultepec	1·4	3·2	5·6	7·10	9·14	11·12	13·8	M
<sup>b</sup> Texmelucan	1·4	3·2	5·6	7·10	9·14	11·12	13·8	M
<sup>b</sup> Toluca	1·4	3·2	5·6	7·10	9·14	11·12	13·8	M
<sup>b</sup> Zimapan	1·4	3·2	5·6	7·10	9·14	11·12	13·8	M
Most common arrangement encountered among races of <i>Oe. hookeri</i> :								
	1·2	3·4	5·6	7·10	9·8	11·12	13·14	H

IV) have been derived through similar reasoning, utilizing the cytological data presented in Table III.

<sup>b</sup>Guatemala

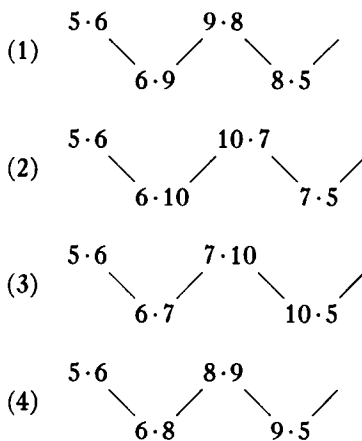
Gives  $\odot^3$  12, 1 pair, with *elongans*; it cannot have any of the following *elongans* chromosomes:

- 1·4, 3·2, 5·10, 7·6 (Gives  $\odot$  10,  $\odot$  4 with *βIowa* 2, which has these chromosomes)
- 9·14 (Gives  $\odot$  8,  $\odot$  6 with *truncans*, which has 9·14)

The pair with *elongans* must, therefore, result from the presence of either 11·12 or 13·8.

Assume that it has 13·8. Gives  $\odot$  4,  $\odot$  4, 3 pairs, with <sup>b</sup>*Johansen*; in this combination one  $\odot$  4 must include 13·8 of <sup>b</sup>*Guatemala*, and, therefore, 9·8 and 13·14 of <sup>b</sup>*Johansen*. <sup>b</sup>*Guatemala* must have 9·14 in order to complete the circle. This is impossible, since <sup>b</sup>*Guatemala* cannot have 9·14, as shown above. Therefore, it cannot have 13·8 and must have 11·12.

Gives  $\odot$  8,  $\odot$  4, 1 pair, with *neo-acuens*. The pair in this combination must result from the presence of 11·12. It cannot, therefore, have 5·6. Gives  $\odot$  8, 3 pairs, with <sup>b</sup>*hookeri* and  $\odot$  4,  $\odot$  4, 3 pairs, with <sup>b</sup>*Johansen*. Therefore, in the combination with <sup>b</sup>*Johansen*, 7·10 must be in one  $\odot$  4 and 9·8 in the other. The 5·6 of <sup>b</sup>*Johansen* must also be in one of these circles. Hence, the circle which includes 5·6 must be one of the following:



- (1) requires that <sup>b</sup>*Guatemala* have 5·8 and 9·6; if this were so, it would give at least two pairs with *αIowa* 2. The observed configuration shows only one pair. (1) is thus eliminated.
- (2) requires that <sup>b</sup>*Guatemala* have 6·10. If it had 6·10, it would give at least two pairs with *βIowa* 6. Hence, (2) is eliminated.
- (3) requires that <sup>b</sup>*Guatemala* have 5·10. It cannot have 5·10, since it gives  $\odot$  10,  $\odot$  4, with *βIowa* 2, which has 5·10. Hence, (3) is eliminated.
- (4) cannot be eliminated. Therefore, <sup>b</sup>*Guatemala* must have 6·8 and 5·9. Gives  $\odot$  12, 1 pair, with *punctulans*.

It cannot have any of the following *punctulans* chromosomes:

- 1·4 (As shown above)
- 11·10 (Gives  $\odot$  8,  $\odot$  6, with *truncans*, which has 11·10)
- 6·12, 7·8 (Since it has 6·8)
- 5·2, 3·9 (Since it has 5·9)

<sup>3</sup> The symbol " $\odot$ " means "a circle of"; thus, for example, " $\odot$  14" means a circle of fourteen chromosomes.

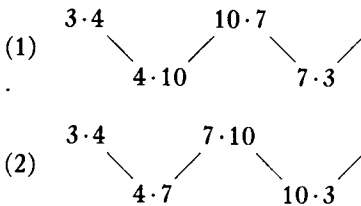
The pair with *punctulans* must, therefore, result from the presence of 13·14.

Gives  $\odot 8$ ,  $\odot 4$ , 1 pair, with *aIowa 2*. It cannot have any of the following *aIowa 2* chromosomes:

- 5·8, 9·6 (Since it has 5·9 and 6·8)
- 7·11, 10·12 (Since it has 11·12)
- 3·14, 13·4 (Since it has 13·14)

Therefore, the pair in this combination must result from the presence of 1·2.

Gives  $\odot 4$ ,  $\odot 4$ , 3 pairs, with <sup>h</sup>*Johansen*. The three pairs result from the presence of 1·2, 11·12, and 13·14. One  $\odot 4$  includes 5·6 and 9·8 of <sup>h</sup>*Johansen* and 6·8 and 5·9 of <sup>h</sup>*Guatemala*. The remaining circle must be one of the following:



<sup>h</sup>*Guatemala* cannot have 3·7, since it gives  $\odot 8$ ,  $\odot 6$ , with *truncans*, which has 3·7. Therefore, (1) is eliminated, and <sup>h</sup>*Guatemala* must have 3·10 and 7·4. Thus,

$$\begin{array}{cccccc} \text{<sup>h</sup>Guatemala} = & 1 \cdot 2 & 3 \cdot 10 & 5 \cdot 9 & & \\ & & 7 \cdot 4 & 6 \cdot 8 & 11 \cdot 12 & 13 \cdot 14 \end{array}$$

This formula gives the correct configuration with all the complexes with which <sup>h</sup>*Guatemala* has been combined, including those mentioned above as well as *jugens* ( $\odot 12$ , 1 pair), *aCamas* ( $\odot 10$ ,  $\odot 4$ ), and  *$\beta$ Camas* ( $\odot 12$ , 1 pair).

#### DISCUSSION

Munz (1949) has recently published a taxonomic treatment of the large flowered forms of the subgenus *Euoenothea* which occur throughout southwestern North America and Mexico. According to this treatment, the forms which have been analyzed in the present study belong to *Oe. elata*. Morphologically, *Oe. elata* shows a strong affinity to *Oe. hookeri* which includes the forms occurring in

northern Mexico and California. In fact, Munz, in speaking of *Oe. elata*, states, "It is questionably distinct from the *hookeri* assemblage from farther north." Both of these species show similar cytogenetic features, namely, seven pairs of chromosomes at meiosis, the absence of lethals, and open pollination.

On the other hand, *Oe. elata* possesses certain characters which distinguish it from *Oe. hookeri*. *Oe. elata* has thicker fruits, heavier buds, shorter styles, and broader leaves which are often stiff and wavy. Moreover, the results of the present analysis show that the two segmental arrangements found among the races of *Oe. elata* are in each case two interchanges removed from the arrangement which is most commonly encountered among the *hookeri* group. The occurrence of distinctive segmental arrangements, therefore, also argues for the validity of these two species.

The *hookeri* group has in the past been considered primitive among North American euoenotheas. The presence of paired chromosomes at meiosis, freedom from lethals, open pollination, all of which characterize *Oe. hookeri*, are considered to be primitive characters. A further indication that the California races are primitive has been shown by Cleland (1949). With 14 pairing ends and 7 chromosomes in a genome, it is possible to have 91 different kinds of chromosomes with respect to the association of pairing ends. If the frequencies of the different kinds of chromosomes in populations of North American euoenotheas are plotted, seven peaks are obtained which coincide with the seven chromosomes which are found in most of the *Oe. hookeri* races. The wide distribution of these chromosomes which have escaped interchange is good evidence that the *hookeri* arrangement is the ancestral type.

Recognition of *Oe. elata* as a group distinct from *Oe. hookeri* in respect to morphology as well as segmental arrangement raises the question as to the position of *Oe. elata* in the phylogeny of the

subgenus. *Oe. elata*, like *Oe. hookeri*, possesses paired chromosomes, lacks lethals, and is open pollinated. On the other hand, it is interesting to note that most of the chromosomes which characterize the *elata* segmental arrangements (e.g. 9·14, 5·9, 13·8, 3·10, 6·8) do not occur with any appreciable frequency among the populations of North American euoenotheras. *Oe. elata*, therefore, cannot be considered ancestral to the North American forms.

The two *elata* arrangements, M and G (table IV), are a minimum of four interchanges removed from each other. Each, however, is only two interchanges distant from the *hookeri* arrangement. In the evolution of these races it seems unlikely that one has been derived directly from the other, since this would involve, in two forms phenotypically very similar, at least four interchanges. According to a more plausible hypothesis the M and G arrangements have arisen from a common ancestral type, namely the *hookeri* arrangement. In the case of each of the *elata* arrangements two different interchanges are involved, but this is not contrary to expectation. There is no evidence that interchanges involving certain chromosomes occur preferentially (Oehlkers and Linnert, 1949). Thus, if an ancestral arrangement undergoes interchanges at various times during its historical existence, one might expect to have produced a group of forms each of which is the result of a different series of interchanges. *Oe. hookeri*, therefore, appears to be ancestral for the Mexican and Central American races of *Oe. elata* as well as for the North American forms of the subgenus.

In the light of the relationships indicated by the segmental arrangements of these forms it is of interest to consider their geographical distribution. According to Munz (1949) *Oe. elata* ranges through the highlands of central Mexico as well as the highlands of Guatemala, although collections from the latter area are few. *Oe. hookeri* extends from north-

ern Mexico into California and the neighboring states. These two closely related species thus occupy adjacent geographical areas. If we accept the hypothesis that *Oe. elata* was derived from *Oe. hookeri* or an essentially similar ancestral type, the latter must have extended throughout Central America, Mexico, and the southwestern United States before *Oe. elata* became differentiated. Since *Oe. hookeri* and *Oe. elata* are at present still completely interfertile, the latter must have become differentiated through some type of isolation. Presumably this isolation was achieved toward northern Mexico by the climatic changes which occurred in this area in past geological periods. That such changes have occurred is well established, although there is some dispute as to when they took place. Epling (Dobzhansky and Epling, 1944) has reviewed evidence bearing upon climatic changes in the entire southwestern and Mexican region and concludes that the trend toward greater aridity began during the Oligocene; by the end of this period the arid vegetation of the north Mexican plateau had appeared and the climate since that time had remained essentially as it is today. Mayr (1945) disputes these conclusions, maintaining that humid cycles occurred in this region during the Pleistocene. Munz (1949) points out that the euoenotheras in the Southwest grow along streams and irrigation ditches and that they cannot be considered members of an arid flora. With the development of an arid climate, therefore, the original *hookeri* or *hookeri*-like population may have been restricted in distribution with populations limited in size and confined to ecologically suitable habitats. The tendency for the originally widespread population to be broken into smaller units could readily have resulted in the development of new forms as localized races in different parts of the entire area.

It is hoped that additional material from this area can be obtained for cytological analysis. Field studies dealing with distribution and ecology of the forms

in this area will also be essential to substantiate the tentative conclusions which are outlined above.

In conclusion, it is of interest to call attention to two points revealed by this study which have a general significance in the cytogenetic approach to problems of phylogeny in *Euoenothera*. It will be noted that races of *Oe. elata* may be as many as four interchanges removed from each other and yet show close morphological similarity. Thus phenotypic changes do not necessarily parallel segmental interchanges in every case. This emphasizes the necessity of correlating cytogenetic evidence with all other available facts, allowing no single type of evidence to serve as an absolute index of phylogeny.

Secondly, these two groups of races illustrate how, with few but divergent interchanges, segmental arrangements can arise which differ sufficiently to produce very nearly a complete translocation heterozygote upon hybridization. Hybrids between Guatemala and any of the other *Oe. elata* races show at meiosis  $\odot 6, \odot 6, 1$  pair. If two such populations which have undergone divergent interchanges come into contact, translocation heterozygotes will occur. If a system of balanced lethals develops concurrently, a true breeding heterozygote is produced. *Oe. elata* thus represents an early stage in an evolutionary sequence which may ultimately lead to the development of true breeding complex heterozygotes similar to those occurring among the North American euoenotheras.

#### SUMMARY

1. A group of races of *Euoenothera* from central Mexico and Guatemala is described. These races belong to the species, *Oe. elata*.

2. These races possess all-pairing chromosomes. The segmental arrangements of their complexes have been determined.

3. Two segmental arrangements occur in these races, both of which indicate a close relationship to *Oe. hookeri*.

4. The nature of the relationship between *Oe. elata* and *hookeri* is discussed. Available evidence supports the earlier conclusion that *Oe. hookeri* is the primitive group among the North American euoenotheras. *Oe. elata* also appears to have been derived from *Oe. hookeri*, or a similar ancestral type.

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