### A REVISION OF GRACE'S WARBLER

## J. DAN WEBSTER

GRACE'S Warbler (Dendroica graciae) is one of the least known of North American parulids. The behavior, ecology, and nest, so far as known, were described by Bent (1953). The races were briefly reviewed by Griscom (1935), including a description of a new race, remota, from Nicaragua. Brodkorb (1940) described a new race, ornata, from Chiapas. Phillips and Webster (1961) have recently described an additional race from Nayarit.

My own investigations involved the collection of several specimens in Mexico, including 20 in fresh plumage in August and September of 1959, and the study of 354 museum skins, most of them on loan to the California Academy of Sciences. I want to thank Dr. Robert T. Orr for his help throughout this study. Drs. Alden H. Miller at the University of California and Robert H. Storer at the University of Michigan were courteously hospitable in the museums they curate. following museums generously loaned me their Grace's Warblers: American Museum of Natural History, British Museum (Natural History), University of California Museum of Vertebrate Zoology, Dickey Collection of the University of California at Los Angeles, Carnegie Museum, Chicago Natural History Museum, Museum of Comparative Zoology of Harvard College, Instituto de Biología of the Universidad Nacional Autónoma de México, Louisiana State University Museum of Zoology, University of Michigan Museum of Zoology, Minnesota Museum of Natural History, Texas A. and M. University, and the United States National Museum. Allan R. Phillips and Lewis D. Yaeger loaned me all the Grace's Warblers from their personal collections. Financial support was received from the National Science Foundation, Grant G8703.

#### RANGE AND ECOLOGY

The breeding range of Grace's Warbler extends from southern Utah, southeastern Colorado, and western Texas south through western Mexico to the Isthmus of Tehuantepec and through Central America, from western Chiapas to northern Nicaragua. The winter range includes the breeding range from Nayarit and Michoacan south and also the Transvolcanic Range of central Mexico east to Volcan Popocateptl. A single record from Veracruz is given in the Mexican Check-list (Miller et al., 1957) as "Breeding, May, K-d" [K-d = specimen in Moore Collection]. See map, Figure 1.

Within the vast range described above, Grace's Warbler inhabits only pine forest, and the pines of pine-oak woodland and forest. More precisely, the range may be stated as: Along the Pacific coastal slopes of Mexico, from Nayarit to western Chiapas, it is resident in humid yellow pine forests at middle elevations of 800-1,800 meters (2,500-5,500 feet). In the southwestern United States and the eastern flank of the Sierra Madre Occidental of Chihuahua, Sonora, Durango, and Zacatecas it breeds in arid Ponderosa Pine, Chihuahua Pine, or Apache Pine forest, and pine-oak woodland, at elevations of 1,800-2,700 meters (5,500 to 8,000 feet). In central Michoacan it is resident under conditions somewhat intermediate between those described in the two preceding sentences—humid pine forest or pine-oak woodland at 1,500-2,500 meters

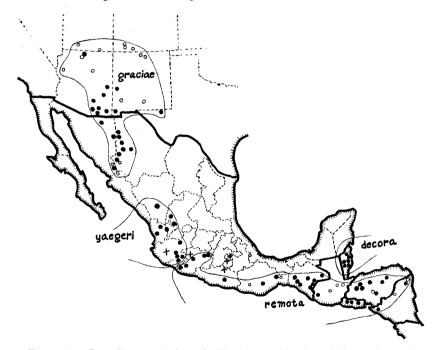


Figure 1. Distribution of Grace's Warbler in North and Central America. Names indicate the subspecies. Narrow, solid lines delimit the ranges of the subspecies. Broad, solid lines mark international boundaries. Dashed lines mark state boundaries in Estados Unidos de México and the United States of America.

Each locality from which a breeding-season specimen was examined in the present study is marked by a solid dot. Each locality where there is a record in the literature is marked by a hollow dot. Each locality from which only a wintering or migrant specimen was examined in the present study is marked by a cross.

(4,500-7,500 feet). In Brutish Honduras and the Caribbean coast of Nicaragua it is resident in humid coastal pine forest near sea level. Ir El Salvador, northwestern Nicaragua, southeastern Chiapas, Guatemala and Honduras it occupies humid pine forests at middle elevations of 650-1,500 meters (2,000-4,500 feet). The predilection of Grace's Warbler for pines is extreme; only twice have I seen one land in an oak tree, and then it was nervous and not foraging. The preferred habitat seems to be a sparse stand of rather small pines, 5-10 meters high. However, I have seen them in closed-crown pine forests where the trees are 25 meters tall. Paynter (1957) saw a few Grace's Warblers in broadleaved trees in mixed pine-broadleaved woodland in Chiapas. His conclusion that pines are not required for the presence of the species is, to my mind, erroneous.

The absence of Grace's Warbler from eastern Mexico, and from the temperate and boreal high pine forests of Estado de Mexico, Oaxaca, and all of Central America is striking. Conversely, the Olive Warbler (Peucedramus taeniatus) is a common to abundant resident in these areas, but is absent from the low-elevation and middle-elevation pines of the Pacific slope of Mexico and all of Central America. (There is some sympatry at middle elevations in Chiapas, at least, for at El Fenix, Monserrate district [see Edwards and Lea, 1955], we found Grace's Warbler common but the Olive Warbler present in small numbers in humid pine forest at 1.550 meters.) In Michoacan, humid pine forest and pine-oak woodland at 2,330-2,660 meters near Patzcuaro and Morelia is inhabited by both species, with the Olive Warbler the more common. In southern Durango, both species are found in the more arid pine fasciation on the eastern flank of the Sierra Madre Occidental, but only the Olive Warbler along the crest of the range. A Grace's Warbler was recently taken in Sinaloa, the first from that state or from the more humid western slope of the Sierra Madre Occidental. An adult male in fresh plumage, it was collected 27 July 1961 by Bill R. Brinkley, in the lowest clump of pines along the Durango-Mazatlan highway, at 1,300 meters, one mile south of Potrerillo. I prepared the specimen, which is now in the Calif. Acad. Sci. In southern Arizona and northern Sonora (Marshall, 1955, and Phillips, pers. comm.) the two species are largely co-resident, though the Olive Warbler ranges somewhat higher. The range of Grace's Warbler extends considerably farther north than does that of the Olive Warbler, the latter not going beyond southeastern Arizona and southwestern New Mexico.

The preceding paragraph was based on my observations in Sinaloa, Durango, Zacatecas, Michoacan, Nayarit, Guerrero, Oaxaca, and Chiapas. Also, it was supplemented by information on many specimen labels and the statements of Marshall (1956) for Arizona and Sonora, Dickey and Van Rossem (1937) for El Salvador, and T. R. Howell (pers. comm.) for Nicaragua.

On migration Grace's Warbler must, occasionally, land in stands of deciduous trees. However, the only such record of which I have knowledge is one taken 14 April 1942 at Taxco, Guerrero, where there are no pines, by M. L. Miles (La. State Univ. specimen).

#### VARIATION

Individual variability in color is moderate, but certain color factors also vary geographically, as for instance hue of the ventral yellow in *decora* and dorsal black streaking in *yaegeri*. Individual variability in wing and tail length is rather great. (See Tables 1 and 2.)

Sexual dimorphism in size is slight but definite; males average larger. As to color, males are more bluish-gray, less brownish than females, with more tendency to black streaking on the back. But this sexual dimorphism in color varies geographically, being consistent and stronger in *graciae* and *decora*, less consistent and slighter in *yaegeri* and *remota*. Sexual dimorphism of fall immatures, *inter se*, is relatively about the same as that of adults. I fail to detect any sexual dimorphism in the juvenal plumage.

In general, fall immatures as compared with adults are slightly browner, with less tendency to dorsal streaking, in the same sex in any one geographic area. In *graciae*, immatures also average smaller and paler yellow below.

I compared 18 skins in the streaked brown juvenal plumage: two of graciae, seven of yaegeri, eight of remota, and one of decora. Differences due to foxing were greater than those due to geography, but it was clear that graciae was more rufescent, less grayish than the more southern races, and that decora was less streaked ventrally than the others.

Study of molts was difficult because: (1) There were only three clear-cut specimens of graciae taken between late September and mid-April. (2) There was a scarcity of aged specimens of all populations. The juvenal plumage is replaced by a partial postjuvenal molt (complete except for the flight feathers) in June or July to July or August. This is a rapid molt, much of it accomplished while the young are still being fed by their parents. Specimens were examined that had completed this molt as early as 14 July (Arizona), 5 July (Guerrero), and 9 August (Honduras).

There may very well be a partial prenuptial molt in the race graciae, but I have not seen such molting specimens. Indirect evidence suggesting the existence of such a molt is the fact that in this race the plumage of the immatures (especially the males) differs distinctly from that of adults in winter plumage, whereas the differences the following May are slight indeed. I have seen no specimens of graciae taken between 21 February and 12 April. In the southern races there is even less evidence for the existence of a prenuptial molt. The postnuptial molt extends from late June, July, or August to August or early September. The earliest taken specimens with aged skulls that had completed the molt were taken 8 August (Michoacan), 9 August (Guerrero), and 3 September (Arizona).

### GEOGRAPHIC VARIATION

Eleven characters in adults and three in immatures were studied. Only fresh-plumaged birds (arbitrarily defined as summer birds over halfway through the postnuptial molt and on through specimens taken 28 January) were used below for color comparisons. Capitalized color names refer to direct comparison with the color standard of Palmer and Reilly (1956).

1. Width of the white area on the inner web of the 3rd rectrix (counting from the outside) was used by Griscom (1935) as a subspecific character. It varies geographically, but not to the extent postulated by Griscom. I was able, consistently, to distinguish only two categories—"wide white" and "narrow white."

	Tail	white	in	fresh-	plumaged	adults
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Race	Sample size	% narrow white
graciae	25	60
yaegeri	14	22
remota (including Michoacan and Honduras)	19	26
decora	4	100

2. Griscom (op. cit.) used the color of the posterior part of the superciliary stripe (white or yellow) as a subspecific character. I found that there was a slight, average tendency for the posterior part of the superciliary stripe to be white in the north and yellow in the south. I counted the fresh-plumaged adult specimens in which there was no white in the posterior part of the superciliary stripe as follows:

Race	Sample size	% with no white
graciae yaegeri remota (incl. Michoacan but excl. Honduras) remota (Honduras only) decora	25 16 21 8 4	0 12 10 50

- 3. According to Ridgway (1902), Griscom (op. cit.), and Brodkorb (op. cit.) the posterior extent of the ventral yellow varies geographically. It is true that in adult males the yellow of the breast extends farther posteriorly (onto the belly) in most Central American specimens than in most U.S. specimens. The variation due to make of skin exceeds that due to geography, however, and I cannot evaluate this character.
- 4. Brodkorb (op. cit.) noted the geographical variation in bill shape, with the comment that it was not adequately represented by measurements. My observations agree with his, and can be tabulated thus:

Slender, subulate	More robust and longer	More robust and shorter
all graciae	about ½ of yaegeri	all of decora
about ½ of <i>yaegeri</i>	all of <i>remota</i> (incl. Michoacan, but excl. Honduras)	all Honduras specimens of remota

Several intermediates, especially of yaegeri and Honduran remota, are difficult to allocate to the above categories.

5. The pale (not streaked) areas of the posterior underparts are suffused with buff in some northern specimens. For the purposes of this table, the intermediate populations of Michoacan and Honduras are lumped with *remota*. Four categories were separable:

Posterior underparts of fresh-plumaged adults

Strongly suffused with pale Buffy <b>Brown</b>	Suffused with very pale Buffy Brown	Weakly suffused with very pale Buffy Brown	White or nearly so
4 graciae 9	7 graciae 9 4 yaegeri 9 14 graciae 8 2 yaegeri 8	2 yaegeri 8	13 remota Q 1 decora Q 8 yaegeri & 16 remota & 3 decora &

6. The dorsum is often streaked more or less heavily with black, with variation both sexual and geographical. Rather obviously segregation of races on this character is erratic. Honduras is included with remota in the table.

Streakiness of back in fresh-plumaged adults

Much, broad	Moderate,	Moderate,	Streaking absent or nearly so
streaking	broad streaking	narrow streaking	
	1 Michoacan	2 graciae ♀	9 grac <b>i</b> ae Q
	remota Q	2 yaegeri ♀	2 yaegeri Q
	2 remota Q	4 remota ♀	6 remota Q
1 Jalisco	10 graciae 3	2 graciae 8	1 decora ♀
vaegeri 3	2 vaegeri 3		2 graciae ♂
2 Michoacan remota A	1 Michoacan remota 3	5 yaegeri & 3 remota & 3 decora &	4 yaegeri 8
3 remota 8	7 remota 3	0 400014 0	

7. The hue of yellow on the throat and breast. In general, there is a smooth cline in each sex from yellower in the U.S. to oranger in British Honduras. Honduras and Michoacan are included with *remota* in the table. However, I made a division into six categories (3 for females and 4 for males):

Hue and intensity of yellow on anterior underparts of fresh-plumaged adults

Pale and yellow	Brighter and orangish yellow	More orangish yellow	Still brighter and yellowish orange yellow*	Deep orange yellow
11 graciae ♀	4 yaegeri ♀		remota Q	
	11 graciae 3	3 graciae & 7 yaegeri &	decora ♀ 2 yaegeri ♂	3 decora 8
	3 yaegeri 3	5 remota 8	11 remota 3	

8. Color of the back is the most variable character, geographically. In fresh-plumaged adult males, a tabular representation is:

Browner ←			$\rightarrow$	More bluish gray
14 graciae	12 yaegeri	3 Michoacan remota	9 "typical" remota	3 decora
Browner and less bluish gray than all others	Paler, warmer, less bluish than remota; warmer and less bluish than	intermediate between yaegeri and "typical" remota	Darker, warmer, less purely blue gray than decora	More purely blue gray than all others
	decora		4 Hondu remota	ras
			More dra than deco less bluisl and paler than remo	ra; n

There is no overlap among the samples of the four races if the Michoacan and Honduras populations are omitted. Of these, both are best regarded as "intermediate, nearest remota"; the Michoacan sample is slightly browner than more "typical" remota, thus tending toward yaegeri; the Honduras variant of remota is more drab, less purely bluish gray than decora, and less bluish and paler than "typical" remota from Chiapas, Oaxaca, and Guerrero.

In fresh-plumaged adult females geographic variation in back color is even greater than in males, but the pattern is not wholly parallel.

<sup>\*</sup> Categories of columns 3 and 4 were not differentiated in females. .

### A tabulation is:

Browner ← → Bluer 1 Michoacan 4 Honduras remotaremota 8 "typical" 11 graciae 4 yaegeri \*1 decora remota Brown; all Slightly More bluish Browner, others more olivaceous. browner, less gray than all more or less bluish bluish gray others less gray than remota than "typical" and decora or Michoacan remota

- 9. Length of wing in adults shows a definite cline from shorter to the south to longer in the north. Measurement was of the chord. Overlap between adjacent races is considerable. Length of wing in females varies in a pattern closely parallel to that in males (see Table 1).
- 10. Length of tail in adults shows a cline very similar to that of the wing length (see Table 2). Wing-tail difference, calculated by subtracting the mean for adult males for tail length from that for wing length, is perhaps more expressive than either simple value. The wing-tail difference to the nearest half millimeter is: U.S. graciae 18; Chih., Son. graciae 17; yaegeri 17.5; Michoacan remota 16; Guer., Oax.

TABLE 1

Length of Wing in Adult Males

Race	Locality	Sample size	Range	Mean	Standard deviation	
graciae	United States	90	62-70	66.54	1.75	2.64
graciae	Chih. and Sonora	33	60-69	64.85	1.61	2.49
yaegeri	Dur., Zac., Nay., Jal.	29	62-69	64.83	1.64	2.53
remota > yaegeri	Michoacan	5	62-65	64.00		
remota	Guer, and Oax.	12	57-65	61.50	1.98	3.22
remota	Chiapas	19	59-66	61.89	1.95	3.15
remota	Guat., Honduras, Nicar., Salvador	34	56-63	59.53	1.56	2.62
decora	Brit. Honduras	17	54-61	57.00	1.81	3.18

<sup>\*</sup>This single specimen of decora in fresh female plumage is probably an extreme. In a similar comparison of worn female material, including 15 decora, four matched the Oaxaca-Chiapas-Salvador-Honduras-Nicaragua series of 26 remota, but 11 were bluer and less brown than any remota, thus paralleling the results on both fresh and worn males and invalidating the above comparison of estingle fresh female. [Worn specimens, of which many more were compared than of the fresh-plumaged birds tabulated above, could usually be sorted into the same categories on the basis of dorsal color and of hue of the ventral yellow.]

TABLE 2
LENGTH OF TAIL IN ADULT MALES

Race	Locality	Sample size	Range	Mean	Standard deviation	
graciae	United States	90	47-53	48.68	1.37	2.82
graciae	Chih. and Sonora	33	44-51	47.82	1.56	3.27
yaegeri	Dur., Zac., Nay., Ial.	28	45-50	47.29	1.19	2.52
remota > yaege <b>ri</b>	Michoacan	5	46-48	47.60		
remota	Guer. and Oax.	11	44-47	45.46	1.08	2.36
remota	Chiapas	19	44-49	46.68	1.41	3.03
remota	Guat., Honduras, Nicar., Salvador	33	43-48	44.61	1.15	2.84
decora	Brit. Honduras	17	41-48	44.29	1.56	3.53

remota 16; Chiapas remota 15; Guat., Hond., Nicar., Salv. remota 15; decora 13.

11. Weights were available on the labels of 84 specimens. However, they were so scattered through the months of the year and the geographic range of the species that no definite pattern could be seen. Range for males was 6.9 to 10.5 g and for females 6.7 to 9.6 g.

Immatures in fresh plumage (July to December) were compared as to color of the back, color of the yellow of anterior underparts, and color of the pale areas of the posterior underparts. There were 27 females of the races graciae, yaegeri, and remota and 36 males of the same three races available; the sexes were compared separately. Differences paralleled those noted above for adults, but were somewhat more clear cut as regards hue of the ventral yellow. Specifically, separation of each of the races was 100 per cent, from 100 per cent for color of the back in both sexes and color of the posterior underparts in males. Separation of the races with slight overlap of extremes was observed for hue of the ventral yellow in both sexes. Color of the posterior underparts in females made a complete separation between graciae and remota, but yaegeri overlapped both other races considerably.

#### DISCUSSION OF TAXONOMY

The race *ornata* was clearly described by Brodkorb (1940) from Chiapas. Unfortunately, Brodkorb did not compare his new race with *remota*, which had been very briefly described by Griscom in 1935, from northwestern Nicaragua, on the basis of eight worn April and May specimens. I borrowed four of the paratypes from the British Museum (through the courtesy of R. W. Sims) and compared them

with the type and many other specimens of "ornata" at the University of Michigan Museum of Zoology. Although topotypes in fresh plumage of remota were not available, the subspecific identity of the two populations (Chiapas and Nicaragua) was very clear. A slight tendency to brownness in the posterior underparts of three of the four paratypes of remota was the only departure noted from the coloration of Salvador, Guatemala, Chiapas, and Honduras birds. I recognize remota, then, not as an isolated race from northwestern Nicaragua, but as a widespread subspecies occupying the Pacific coast of southern Mexico plus most of Central America.

I recognize all of the other races of *Dendroica graciae* that have been described. The reluctance of Miller *et al.* (1957: 253) to recognize *ornata* as distinct from *decora* is no doubt due to misunderstanding of the respective ranges involved.

### RESUME OF THE SUBSPECIES

### Dendroica graciae graciae Baird

Dendroica graciae Baird 1865, Rev. American Birds, sign. 14, p. 210 (Fort Whipple, Arizona)

Diagnosis. Back and posterior underparts browner than in all other races. Yellow of throat and breast paler and less orange than in all other races. Dorsal black streaks broader and commoner than in yaegeri and decora, but fewer and narrower than in remota. Bill more slender and subulate than in all other races. Wing and tail longer than in all other races.

Range. Breeds in pines from southern Utah, southeastern Colorado, and western Texas south through the Sierra Madre Occidental of Chihuahua and eastern Sonora to southern Chihuahua (Sierra del Nido). Three clear-cut winter specimens were examined: Amecameca, state of Mexico, 28 January 1943 (La. State Univ.); five km north of Tres Marias, Morelos, 20 December 1948 (Texas A. & M. Univ.); 10 km west of Tepic, Nayarit, 21 February 1955 (Phillips collection). A male from Taxco, Guerrero, 14 April 1942 (La. State Univ.) is a migrant or vagrant but not certainly distinguishable between graciae and yaegeri.

## Dendroica graciae yaegeri Phillips and Webster

Dendroica graciae yaegeri Phillips and Webster 1961, Auk, 78:551 (Cerro San Juan, west of Tepic, Nayarit)

Diagnosis. Back bluer, less brown, than in graciae, but browner and less bluish (adult males also paler) than in remota. Posterior underparts

less buffy than in graciae, but more buffy than in remota. Throat and breast brighter and more orange than in graciae, but duller and more yellowish than in remota. Dorsal black streaks fewer and narrower than in either graciae or remota.

Range. Breeds in pines of eastern flank of Sierra Madre Occidental in southern Durango and western Zacatecas; also more coastal ranges in southern Sinaloa, Nayarit and western Jalisco. Winter specimens were examined from near Tepic, Nayarit; near Autlan, Jalisco; and (migrant or vagrant) near Patamban, Michoacan, 28 January 1903 (U.S. Nat. Mus.). As noted above, a specimen from Guerrero is a migrant or vagrant of either graciae or yaegeri.

# Dendroica graciae remota Griscom

Dendroica graciae remota Griscom 1935, Ibis, p. 548 (Volcan Viejo, Chinandega, Nicaragua)

Diagnosis. Back darker than either yaegeri or decora, browner and less purely blue gray than decora, but more bluish than yaegeri. Posterior underparts indistinguishable from those of decora, but whiter and less suffused with buffy than those of yaegeri. Throat and breast brighter and a more orangish hue of Yellow than in yaegeri, but paler and a more yellowish Orange Yellow than in decora. More and broader dorsal black streaks than in any other race.

Range. Resident in pines of mountains of Michoacan (Patzcuaro, 19 km east of Morelia, 19 km west of Hidalgo) and southwest in the Pacific coastal slope pines of Guerrero, Oaxaca, Chiapas, Guatemala, and Salvador; also across Central America in middle-elevation and low-elevation pines in Chiapas (Laguna Ocotal), Guatemala (Sierra de las Minas), Honduras (Cerro Cantoral, San Esteban, etc.), and Nicaragua (Volcan Viejo).

There is more variation within remota than within any of the other races here recognized. To the north, the Michoacan population shows considerable tendency toward yaegeri, especially in size and hue of the ventral yellow and also is more heavily streaked with black dorsally than any other population of the species. To the south, the Honduras population (and probably that of northwestern Nicaragua, if freshplumaged specimens were available) shows a tendency toward decora in shortness of the bill and slightly less dorsal streakiness; the same population shows an independent trend in another direction, being slightly more brown or drab than more northern populations of remota.

A single February specimen from the northeastern coast of Nicaragua (UCLA) from pines at an elevation of 33 meters has the color of

decora but the size of remota. More specimens in fresher plumage from this area will be necessary in order to settle the racial identity of the population.

# Dendroica graciae decora Ridgway

Dendroica graciae, var. decora Ridgway 1873, Amer. Nat., 7, p. 608 (Belize, British Honduras)

Diagnosis. Back more purely gray than in any other race. Posterior underparts indistinguishable from those of *remota*. Throat and breast a deeper, more orangish orange-yellow than in any other race. Streakiness of the back less than in *remota* and *graciae*, but about the same as in *yaegeri*. Bill relatively short but robust. Wing and tail averaging shorter than in any other population.

Range. Resident on the "pine ridges," near sea level, along the coast of British Honduras.

Breeding or Resident Specimens Examined (Wintering and migrant specimens are listed above.)

D. g. graciae—Arizona 110; New Mexico 11; Texas 4; Sonora 3; Chihuahua 49. D. g. yaegeri—Durango 4; Zacatecas 4; Nayarit 20; Jalisco 13; Sinaloa 1. (Includes all the cotypes of D. g. yaegeri Phillips and Webster.)

D. g. remota—Michoacan 12; Guerrero 18; Oxaca 7; Chiapas 37 (including type of D. g. ornata Brodkorb); Guatemala 1; El Salvador 9; Honduras 38; Nicaragua 5 (including 4 paratypes of D. g. remota Griscom).

D. g. decora-British Honduras 34.

#### SUMMARY

Grace's Warbler has a more or less clinal pattern of variation along a long, narrow, northwest-southeast range, from Utah to Nicaragua in pine forests. Four races are recognized, each with a fairly extensive range. Migration is long in the northern race, short and variable in the next race, and lacking in the two southern races.

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