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STATUS OF CERTAIN FOX SQUIRRELS
IN MEXICO AND ARIZONA

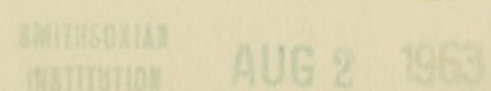
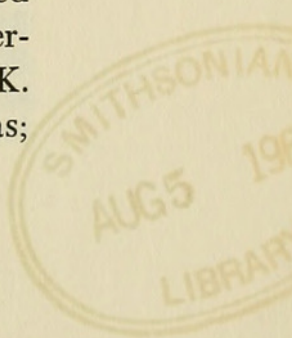
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The *Sciurus nayaritensis* group of fox squirrels previously was composed of three nominal species—*Sciurus chiricahuae* Goldman, 1933, *Sciurus apache* J. A. Allen, 1893, and *Sciurus nayaritensis* J. A. Allen, 1889. These squirrels inhabit the mixed pine-oak forests of the Chiricahua Mountains in Arizona and the Sierra Madre Occidental of Mexico southward as far as southern Jalisco.

In the course of investigations of mammals of the Southwest, we were confronted with the problem of the relationships and taxonomic status of *S. chiricahuae*. Goldman (1933: 72) regarded certain differences between *S. chiricahuae* and *S. apache* and the complete geographical isolation of the former as sufficient evidence for regarding the two as specifically distinct. He stated, however, that they are obviously very closely related. Other authors have also indicated that these forms are related and in fact may be only subspecifically distinct (Hall and Kelson, 1959: 392). Earlier descriptions of *S. chiricahuae* and *S. apache* indicated that differences in size—external and cranial—were of lesser importance than were those of shape and proportions of the skull and coloration. No one subsequently has examined an adequate number of specimens to verify these contentions. Finally, our interest in the taxonomic relationship of *S. chiricahuae* and *S. apache* also has led us to reevaluate the position of *S. nayaritensis*, whose range is complementary to that of *S. apache*.

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David H. Johnson, U. S. National Museum; Rollin H. Baker, The Museum, Michigan State University; William H. Burt, Museum of Zoology, University of Michigan; Richard H. Manville, U. S. Fish and Wildlife Service, Bird and Mammal Laboratories. The figures were prepared by Harry C. Henriksen. This research was supported by the National Science Foundation, grant G-19392.

All measurements are in millimeters. Specimens were used for measurement and comparisons if permanent Pm⁴ was completely erupted. Averages of selected measurements, location of collecting stations, and sample sizes are shown in Table 1. Not all measurements discussed are shown in Table 1.

In order to more clearly present our findings on the relationships among these three kinds of squirrels, we have dealt with the matter as two problems: an evaluation of *apache* and *chiricahuae* and an analysis of *apache* and *nayaritensis*.

COMPARISON OF APACHE AND CHIRICAHUAE

External and cranial measurements: External size varies but little from the Chiricahua Mountains (A) on the north to near the southern limits near El Salto, Durango (F) (see Table 1 and Fig. 1). In length of tail and length of hind foot the Chiricahuan population is smallest but the difference is not marked. A clinal trend is suggested in length of hind foot. Total length is slightly greater in the southernmost populations but again the difference is not great.

Skull measurements indicate an increase in length (basilar, greatest length, and condylobasal) from north to south (see Table 1). Also, the skull tends to decrease in relative breadth (using zygomatic breadth, breadth of rostrum, and postorbital constriction) from north to south (see Table 1), causing a moderate elongation and narrowing of the skull from the Chiricahua Mountains (A) to El Salto (F). None of these gradients is of large magnitude nor is there a strong break within them. A moderate break does appear in most characters between samples A and B (Table 1).

Conformation of skull: Most specimens of *chiricahuae* (A) can be distinguished from most of those of *apache* (B, C, D, E, and F) in having a shorter and broader rostrum and both bulbous and laterally expanded distal ends of nasals. This last condition is also reflected in the larger apertures of the external nares and more concave lateral margins of the nasals in *chiricahuae*. Specimens of *chiricahuae* usually show a more prominent convexity of the anterior region of the frontals. With regard to the aforementioned characters, specimens of *apache* from more northern localities (B and C) exhibit the closest approach to *chiricahuae* while

those from the southernmost localities (E and F) least resemble *chiricahuae*. For example, in dorsal profile and shape of margins of nasals, some specimens from the San Luis Mountains, Chihuahua (B, Fig. 1), are indistinguishable from *chiricahuae*. One specimen from near Colonia García, Chihuahua (C, Fig. 1), also resembles *chiricahuae* in shape of nasals. A specimen from near Huachinera, Sonora (C, Fig. 1), has inflated nasals as in *chiricahuae*. None of these characters is well demonstrated in specimens from areas D, E, and F.

Color: Specimens of *chiricahuae* differ from the majority of those of *apache* in having the underparts (see Fig. 2), orbital ring, and postauricular areas a richer, darker ochraceous. Examination of 45 adult specimens of *S. apache* from several localities within its range shows them to vary considerably. Eight of these specimens are indistinguishable from those of *chiricahuae*; 30 specimens are perceptibly (but only slightly) lighter, and 7 specimens are markedly lighter. Thus, the supposed distinctive coloration of *chiricahuae* is encompassed by the range of variation in color of *apache*.

Remarks: At present it is unlikely that genetic exchange occurs between populations of *chiricahuae* and those of *apache*. The intervening terrain between their ranges creates entirely unsuitable habitat for these squirrels. It is likely that within the range of *apache* there are similar cases where no genetic interchange occurs because of local isolation. However, the close relationship between *chiricahuae* and *apache* is quite obviously shown by the considerable number of characters of *chiricahuae* which appear in varying frequencies within populations of *apache*. In fact, there is no single character of *chiricahuae* which cannot be duplicated in some specimens of *apache*.

Further evidence of close relationship is afforded by the apparent fact that most of the cranial characters of *chiricahuae* are simply the terminal expressions of clinal tendencies within the range of *S. apache*.

COMPARISON OF APACHE AND NAYARITENSIS

External and cranial measurements: In total length, specimens of *apache* and *nayaritensis* average almost the same (556.8 vs. 557.3). However, length of tail averages less and length of body averages more in *nayaritensis* than in *apache* (see Table 1). The hind foot averages very slightly shorter in *nayaritensis* than in *apache*.

Cranial measurements indicate a very slight increase in length, especially basilar length (also nasal, condylobasal, and palatilar lengths), and decrease in width (postorbital and interorbital) in *nayaritensis* when compared to *apache* (see Table 1). None of these differences is judged to be of significant taxonomic value. Most notable is the difference in interorbital breadth (21.26 in *apache*; 20.70 in *nayaritensis*) which is statistically significant ($P = .01-.001$) but which in itself is of little taxonomic value. The differences between the skulls of *apache* and *nayaritensis* are considerably fewer than those between *apache* and *chiricahuae*.

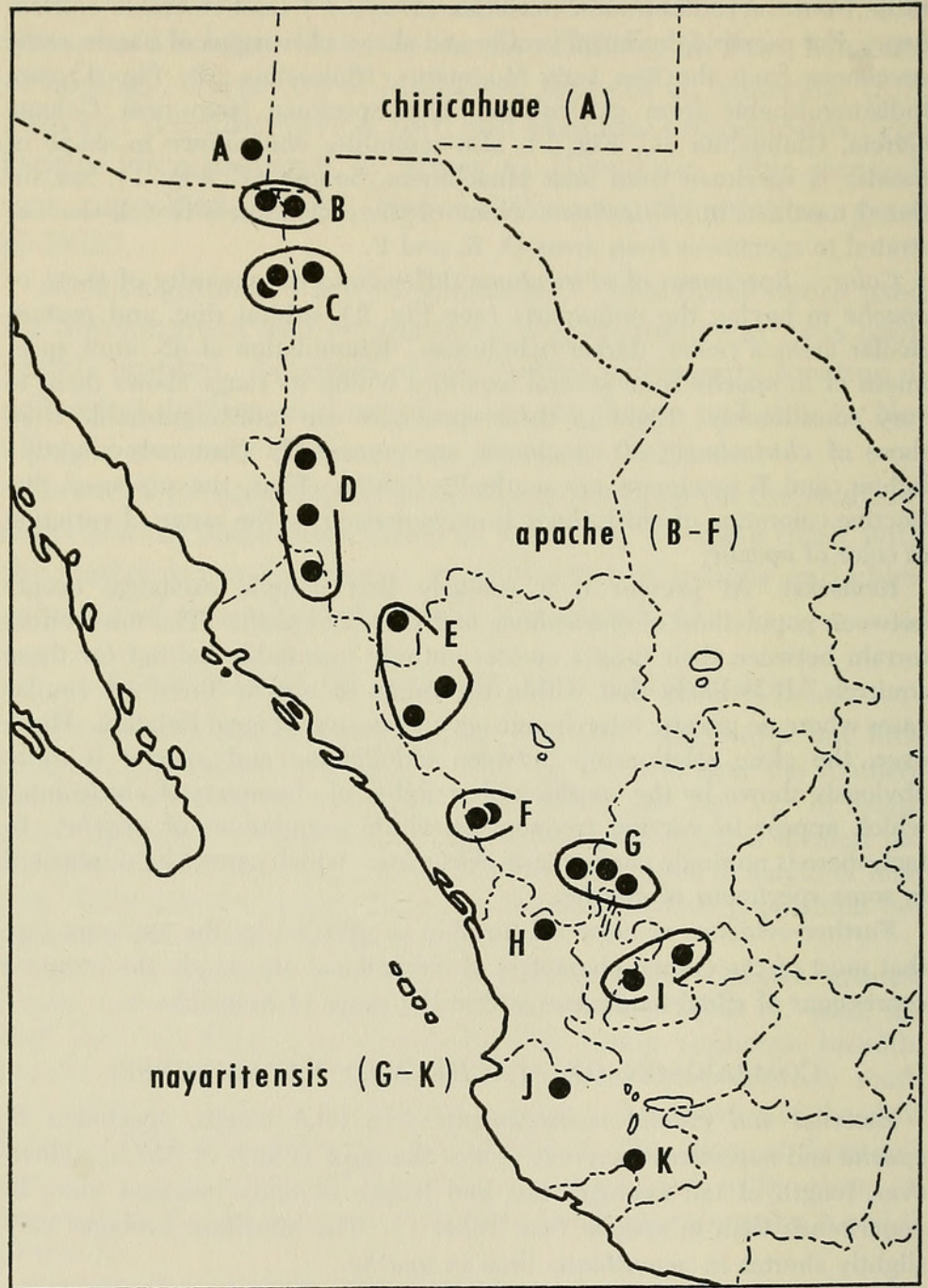


FIG. 1. Solid circles indicate localities from which specimens have been examined. For statistical purposes, specimens from nearby localities were combined. These groupings are indicated by letters which correspond to those in Table 1.

In shape of nasals and dorsal profile, specimens of *nayaritensis* are indistinguishable from *apache*. Specimens of *nayaritensis* do have slightly longer auditory bullae than those of *apache*.

Color: The difference in coloration between *apache* and *nayaritensis*

TABLE 1.—Average external and cranial measurements of *Sciurus nayaritensis* group; locality letters correspond to those on map (Fig. 1)

LOCALITY	N	LENGTH BODY	LENGTH TAIL	LENGTH HIND FOOT	BASILAR LENGTH	ZYGOMATIC BREADTH	POST- ORBITAL BREADTH	LENGTH NASALS	PALATILAR LENGTH	ALVEOLAR LENGTH MOLARS
A	14	282.6	263.9	75.1	48.55	37.87	21.24	21.06	27.51	11.75
B	8	277.1	277.9	77.0	49.94	36.67	20.43	21.96	27.98	12.06
C	7	281.7	273.8	76.3	49.64	37.20	20.90	21.56	27.95	11.99
D	6	282.8	274.8	78.2	50.16	38.31	20.93	22.09	27.97	12.00
E	4	—	—	—	50.08	37.43	19.80	21.88	28.20	11.85
F	14	283.7	274.2	77.9	50.33	37.54	20.17	21.66	28.00	12.04
G	25	287.7	266.9	76.1	50.27	37.31	20.18	21.84	28.19	12.07
H	7	284.0	278.6	79.2	50.41	37.98	20.25	22.17	28.31	12.15
I	9	289.4	270.6	77.3	50.32	37.57	20.41	21.88	27.81	12.15
<i>chiricahuae</i>										
av.	14	282.6	263.9	75.1	48.55	37.87	21.24	21.06	27.51	11.75
s.		± 9.89	± 8.50	±2.98	±0.88	±0.50	±0.36	±0.55	±0.41	±0.21
min.		267	250	71	47.5	37.2	20.5	20.0	26.8	11.3
max.		301	281	80	50.6	38.7	21.9	21.9	28.3	12.2
<i>apache</i>										
av.	39	281.8	275.0	77.5	50.03	37.48	20.46	21.77	27.98	12.02
s.		±10.60	±10.00	±2.60	±0.98	±0.87	±0.64	±0.87	±0.62	±0.28
min.		258	259	73	48.5	35.1	19.4	20.1	26.7	11.2
max.		309	298	82	52.5	39.9	21.6	23.7	29.2	12.5
<i>nayaritensis</i>										
av.	41	287.4	269.9	77.0	50.31	37.48	20.27	21.91	28.10	12.10
s.		±11.55	±12.40	±2.99	±1.09	±0.86	±0.62	±0.79	±0.74	±0.33
min.		264	237	70	48.0	35.7	19.2	20.4	26.3	11.5
max.		315	294	84	52.7	39.1	21.7	23.7	30.4	13.0

is considerable. Dorsally, *apache* is blackish washed with buff or yellow whereas *nayaritensis* is grayish washed with white. In *apache* the hairs of the dorsum have a subterminal black band followed by a buffy band. In *nayaritensis* the hairs are white-tipped (some specimens have a middorsal patch with rusty-tipped hairs) with a subterminal black band followed by a prominent rusty band. In both kinds the hairs basally are dark plumbeous. The upper forearms and hind legs of *apache* are strongly ochraceous-buff compared with mostly grayish limbs (with slight wash of light buff) in *nayaritensis*. Differences in the tail are the broad, white lateral margins in *nayaritensis* compared to the buffy margins in *apache*. The tail of *apache* in the midventral region is usually bright ochraceous compared to hazel in *nayaritensis* (see Fig. 2). The light-tipped hairs are more numerous on the ventral surface of the tail in *nayaritensis*. The underparts in *apache* vary from light buff to bright ochraceous and rarely dark ochraceous. The underparts in *nayaritensis* are usually whitish or rarely (2 of 60 specimens) ochraceous-buff to ochraceous cinnamon. The dark underparts and feet in these two are of a slightly different color than

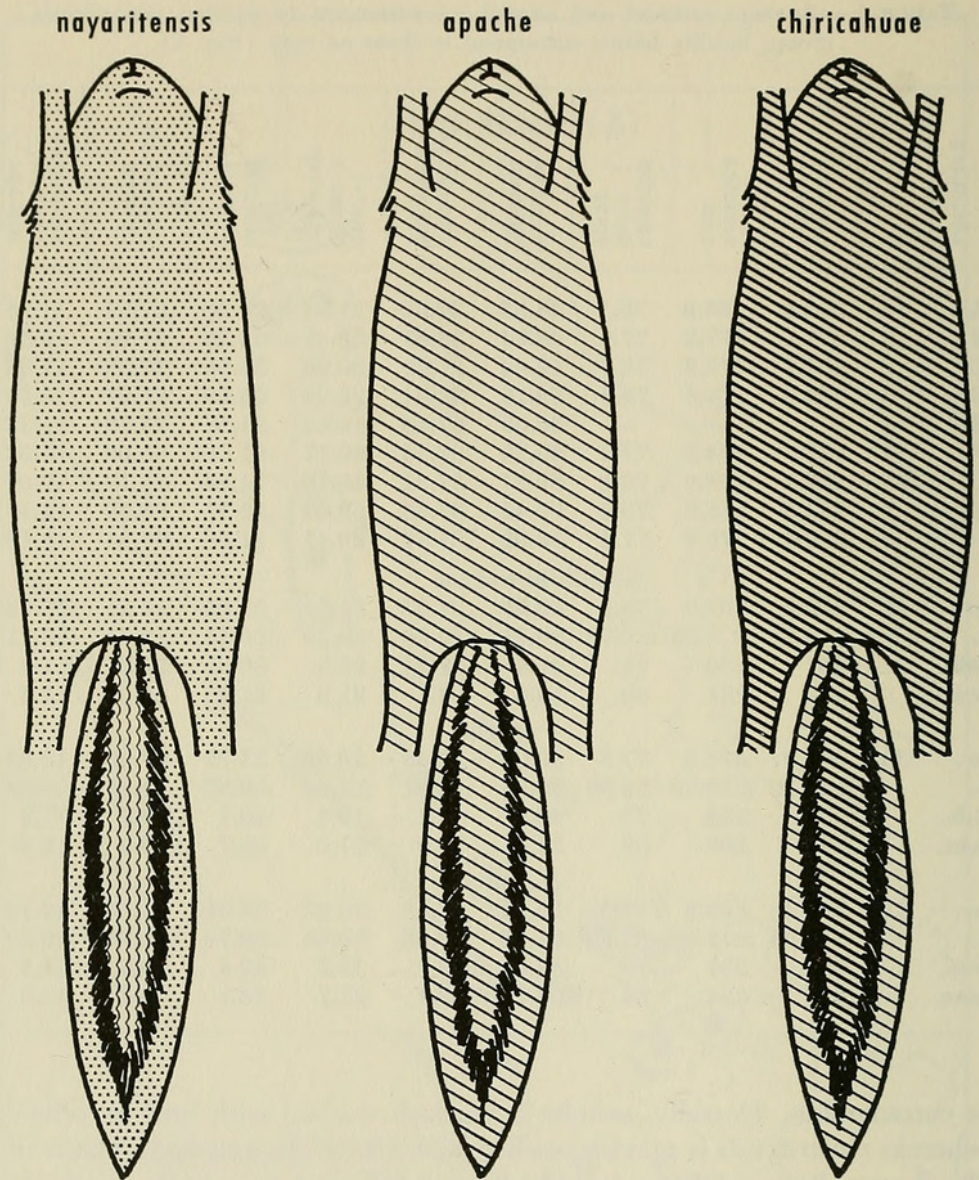


FIG. 2. Diagrammatic, ventral views showing coloration and color-patterns in *nayaritensis*, *apache*, and *chiricahuae*. Dots represent whitish; straight lines, ochraceous (closeness of lines proportional to intensity); wavy lines, hazel; black, black.

in *apache* but distinctly reminiscent of certain specimens of *apache*. We do not regard these two specimens as geographic intergrades. However, they do demonstrate that the genetic basis of the color pattern which is characteristic of *apache* and *chiricahuae* is also present, albeit at a low frequency, in the gene pool of *nayaritensis*.

Remarks: No taxonomically significant differences were found between the skulls of *apache* and *nayaritensis*. Certainly, on the basis of their skulls, the two do not constitute even good subspecies. In fact, the similarity of skulls of these two kinds seems anomalous in view of the striking differences in color.

The form *nayaritensis* seems to exhibit a continuation of certain clinal trends running from *chiricahuae* through *apache*. Although the changes from *apache* to *nayaritensis* are slight, the skull does appear to become still longer and narrower (see Table 1). External size, however, does not show even these weak clinal tendencies. Length of body in *nayaritensis* exceeds that in both *apache* and *chiricahuae* while length of tail and length of hind foot average smaller than those in *apache* but larger than those in *chiricahuae*.

The Río Mesquital, which traverses the entire width of the Sierra Madre in southern Durango, is probably the southern boundary of *apache* and the northern limit of *nayaritensis* (also see Baker and Greer, 1962). No specimens are known of either "species" to indicate otherwise. However, it should be pointed out that no specimens of either of these kinds of squirrels are known from areas immediately adjacent to the river. From published information regarding their habitats, it appears that there are no important differences, if any, among these squirrels. All live in mixed pine-oak woodlands (Baker and Greer, 1962: 86; Nelson, 1899). Direct intergradation between *apache* and *nayaritensis* at present is highly unlikely. Baker and Greer (1962: 37, 51) and also Leopold (1959: Fig. 6) indicate that much of the valley of the Río Mesquital in the Sierra Madre supports a tropical vegetation.

DISCUSSION

That the three kinds, *chiricahuae*, *apache*, and *nayaritensis*, are phylogenetically closely allied is quite indisputable. Sufficient evidence is available to show conspecificity of *apache* and *chiricahuae*. Any reluctance to regard the three as a single species stems solely from the distinctive color of *nayaritensis*. Genetic exchange which in all likelihood has occurred between *apache* and *nayaritensis* should still be evident in intermediate specimens in present populations of these forms. No specimens of *apache* have been examined which would suggest any similarity to *nayaritensis* in coloration. However, two specimens of *nayaritensis* do have the dark ventral coloration suggestive of *apache*.

In view of the great similarity in cranial features between *nayaritensis* and *apache* and notwithstanding the difference in color between the two kinds, we suggest that the two be regarded as conspecific. This conclusion receives support from the findings of other students of variation in the family Sciuridae. Harris (1937) considered a group of taxa, some of which differ strikingly from each other in coloration, to belong to one species, *Sciurus variegatoides*. Banks (1931) concluded that a group of squirrels (*Callosciurus prevosti*) occurring in Sarawak were conspecific although color differences between certain forms were very outstanding and no intergradation was demonstrable between certain subspecies. Nelson (1899) synonymized a group of forms under the name *Sciurus poliopus* although color variation between certain subspecies was extreme. Within the species *Sciurus niger*, which is closely allied to the *nayaritensis* group, spectacular differences occur between subspecies, as for example,

between *S. niger niger* and *S. n. rufiventer*. As a matter of fact, a high degree of intraspecific color variation is not unusual in Mexican and Central American tree squirrels (viz., *Sciurus socialis*, *S. yucatanensis*, *S. oculatus*, *S. poliopus*, *S. deppei*) and is probably the general rule.

Careful evaluation will likely reveal a close relationship between *S. nayaritensis*, as herein delimited, with the species *S. oculatus* and even *S. alleni*. Possibly the similarities are sufficient to justify the inclusion of all these forms under one specific name although we have not critically studied *oculatus* or *alleni*.

Actually, *Sciurus nayaritensis* is closely allied with *Sciurus niger*. The resemblance of skulls and color in *nayaritensis* (especially the color in *apache* and *chiricahuae*) is close to the *rufiventer*-group of *S. niger* (as delimited by Lowery and Davis, 1942: 154) with their smaller skulls and orange-cinnamon or yellowish underparts. The skulls of *S. nayaritensis* differ from those in this group most prominently in more inflated braincase, especially far posteriorly, slightly larger auditory bullae, and greater naso-frontal inflation. The range of variation within the species *Sciurus niger* as presently understood is so great that many workers may regard the differences between *S. nayaritensis* and *S. niger* as those of only subspecific degree.

In light of our present investigation, we feel confident that the following nomenclatural arrangement is warranted:

Sciurus nayaritensis nayaritensis J. A. Allen

1889. *Sciurus alstoni* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 2: 167, 21 October, type from Sierra Valparaíso, Zacatecas. Not *Sciurus alstoni* Anderson 1879 [= *Callosciurus alstoni*], type from Borneo.
1890. [*Sciurus*] *nayaritensis* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 2: vii, footnote, February, a renaming of *S. alstoni* J. A. Allen, 1889.

Specimens examined: Total, 63, as follows: DURANGO: Rancho Las Margaritas, 8350 ft, 28 mi. S, 17 mi. W Vicente Guerrero, 12 (MSU). ZACATECAS: Sierra Madre, 8500 ft, 1 (US); Sierra Valparaíso, 8200 ft, 8700 ft, 4 (AM), 19 (US); Plateado, 8500 ft, 12 (US). AGUASCALIENTES: Sierra Fría, 7500–8200 ft, 3 (MU). NAYARIT: Santa Teresa, 6800 ft, 9 (US). JALISCO: Sierra de Nayarit, 1 (AM); La Laguna, 5000 ft, Sierra de Juanacatlán, 1 (US); Agosto nr. Atenquiqui, 1 (US).

Sciurus nayaritensis apache J. A. Allen

1893. *Sciurus apache* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 5: 29, 16 March, type from western slope of the Sierra de Nacori, 6300 ft, in eastern Sonora.

Specimens examined: Total 53, as follows: CHIHUAHUA: Devils Cañon, 3 mi. SE Mon. 66, 1 (UI); San Luis Mts., Mexican Boundary line, 9 (US); 20 mi. W Casas Grandes, 1 (KU); 3 mi. SW Pacheco, 2 (KU); Río Gavilán, 9 mi. SW Pacheco, 1 (KU); 25 mi. (?) W Colonia García, 1 (US); Sierra Madre Mts., head of Yakui [= Yaqui?], 1 (US); Mojara-

chic, 1 (US); 3 mi. NE Temoris, 3 (KU); near Guadalupe y Calvo, 2 (US). SONORA: about 3 mi. from New Mexico line, SE of Cloverdale, 1 (US); 4 mi. N Huachinera, 1 (US); 4 mi. SW Huachinera, 1 (US); western slope of Sierra de Nacori, about 29 trail miles NE Nacori, 6300 ft [not head Río Bavispe, Chih., see Burt, 1938: 38-39], 1 (US). DURANGO: Arroyo de Bucy, 3 (AM); Ciénega Corrales, 1 (AM); La Ciénega de las Vacas, 1 (AM); El Salto, 17 (US); 3 mi. E La Ciudad, 1 (UI); Laguna del Progreso, 1 (AM). SINALOA: 50 mi. NE Choix [= about 19 mi. E Choix], Sierra de Choix, 3 (US).

Sciurus nayaritensis chiricahuae Goldman

1933. *Sciurus chiricahuae* Goldman, Proc. Biol. Soc. Wash., 46: 71, 27 April, type from Cave Creek, Chiricahua Mts., Cochise County, Arizona.

Specimens examined: Total, 14, as follows: ARIZONA: Pinery Canyon, 4 (US); Fly Park, 1 (US); Green House Canyon, 1¼ mi. E Fly Park, 2 (UI); 4¼ mi. W Research Station, 1 (UI); Herb Martyr Dam, 1 (UI); Cave Creek, 5200 ft, 5 (US).

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