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A NEW INSULAR SUBSPECIES OF THE SPECKLED RATTLESNAKE

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The recent establishment by the San Diego Society of Natural History of a field station at Bahía de los Ángeles, on the west shore of the Gulf of California, has greatly facilitated collecting in central Baja California and on adjacent islands. This has been particularly true of Isla Ángel de la Guarda, one of the largest of the Gulf islands, which lies about 20 miles offshore from the field station.

It has long been known that the speckled rattlesnakes, *Crotalus mitchelli*, found on the island reach a large size — larger than in any mainland section of the extensive range of the species in Baja California and the southwestern United States. Although the presence of this snake on the island has been known for more than 80 years (Streets 1877), until recently only six specimens had been available — not enough to judge the validity of any differences from the mainland rattlers. Now an additional 15 specimens are at hand, besides an unborn brood of eight in which some characters may be ascertained. Not only is the impressive size difference still in evidence. but divergences of squamation and pattern are also apparent. Although no invariable key character has been detected, the differences from the mainland subspecies are sufficiently consistent and significant to warrant the description of the island form. My reasons for placing such insular forms in subspecific categories, despite the virtual impossibility of gene flow, have already been presented (Klauber 1956, p. 28). Therefore I name the form

Crotalus mitchelli angelensis subsp. nov.

ANGEL DE LA GUARDA ISLAND SPECKLED RATTLESNAKE.

- 1877. Crotalus pyrrhus, Streets, Bull. U.S. Nat. Mus. 7:39.
- 1882. Crotalus pyrrhus (part), Yarrow, Bull. U.S. Nat. Mus. 24:73.
- 1883. Crotalus confluentus mitchellii (part), Garman, Mem. Mus. Comp. Zool. 8 (3):173.
- 1887. Crotalus mitcheli (part), Belding, West Am. Sci. 3 (24):98.
- 1889. Crotalus pyrrhus, Townsend, Proc. U.S. Nat. Mus. 13 (800):143.
- 1891. Crotalus pyrrhus (part), Stejneger, West Am. Sci. 7 (59):165.
- 1891. Crotalus pyrrhus (part), Cope, Proc. U.S. Nat. Mus. 14 (882):694.
- 1894. Crotalus mitchellii (part), Van Denburgh, Proc. Calif. Acad. Sci. ser. 2, 4:450.
- 1896. Crotalus mitchelli (part), Boulenger, Cat. Snakes Brit. Mus. 3:580.
- 1929. Crotalus tigris mitchellii (part), Amaral, Bull. Antivenin Inst. Am. 2:82.
- 1930. Crotalus confluentus mitchellii (part), Klauber, Trans. San Diego Soc. Nat. Hist. 6 (3):108, 128.
- 1936. Crotalus mitchellii pyrrhus (part), Klauber, Trans. San Diego Soc. Nat. Hist. 8 (19):157; (20):191.
- 1952. Crotalus mitchelli pyrrhus (part), Klauber, Bull. Zool. Soc. San Diego 26:117.
- 1956. Crotalus mitchelli pyrrhus (part), Klauber, Rattlesnakes 1:38.

TYPE SPECIMEN. — No. 51994 in the collection of the San Diego Society of Natural History. Collected about 4 miles southeast of Refugio Bay, at 1500 feet elevation, Isla Ángel de la Guarda, Gulf of California, Mexico (near $29^{\circ} 291/2'$ N, $113^{\circ} 33'$ W), March 22, 1963, by Dr. Reid Moran.

DIFFERENTIAL DIAGNOSIS. — A subspecies of *Crotalus mitchelli* differing from the other subspecies in its larger size, proportionately larger head in adults, smaller initial rattles, greater number of dorsal scale rows, higher number of ventral scutes, greater frequency of supraoculars with sutures, larger and fewer scales between the prenasals and rostral, and higher number of middorsal blotches on the body. In nearly all of these characters there is some overlapping with the mainland subspecies, but the differences are statistically significant.

DESCRIPTION OF THE HOLOTYPE. — An adult male. Length overall, as measured before shrinkage in preservative, 1331 mm.; tail length 100 mm. or $7\frac{1}{2}$ per cent; length of head (somewhat damaged in killing the snake) 62 mm., contained $21\frac{1}{2}$ times in the body length overall.

The scale rows number 25–27–21, with 15 at the middle of the tail. All dorsals are keeled, except the row next the ventrals on each side. Paired apical scale pits are evident on the posterior dorsals. The ventrals number 185 and the subcaudals 27. The anal is entire. Ten irregular scales border the rattle, which comprises an incomplete string of seven segments; the dorso-ventral width of the proximal lobe is 15 mm.

The supralabials number 14–12, and the infralabials 14–15. The last supralabials are somewhat longer than the others. The first infralabials are undivided; there are neither intergenials nor submentals. The rostral is triangular and is wider than high. As is usual in *C. mitchelli* subspecies, the scales on the snout and crown are so subdivided as to make it difficult to determine to which categories some should be assigned. There is no line of demarcation between the scales of the prefrontal and frontal areas; there are about 26 scales in the prefrontal section, and five scales comprise the minimum intersupraocular bridge.

As is generally the case in *C. mitchelli* subspecies (except *stephensi*), the prenasals do not touch the rostral; however, the separation is not produced by granules but by a single scale on each side having approximately the same height as the prenasal. Besides these scales, the first supralabials and a pair of small internasals contact the rostral. The prefoveals number 8–7.

Each supraocular is sutured by short seams at the outer edge. The scales anterior to the orbit on each side cannot be as readily classified as in most rattlesnakes; it may be said either that the normal upper preocular is divided both horizontally and vertically, and that there are two loreals on each side, or that there are three preoculars and four loreals. The usual crescentic lower preoculars bordering the pit above almost fail to reach the orbit. There are three rows of scales between the supralabials and orbit. The anterior scales on the crown are somewhat knobby; the posterior ones are flat and keeled.

The head is pink above, with ill-defined and irregular fawn blotches. No lateral head stripes are evident. The underside of the head is tan. Dorsally, the body pattern comprises a series of 36 somewhat ill-defined hexagonal, fawn or vinaceous blotches on a pink ground color, with a secondary series of blotches on either side. Posteriorly, the dorsal blotches engage the secondaries and become cross stripes. The dorsum is liberally sprinkled with darker dots, especially within the blotches; these punctations are characteristic of *C. mitchelli* subspecies (except *stephensi*) and give these snakes the name of speckled rattlesnakes. The scales comprising the anterior row bounding the dorsal blotches are often tipped on their posterior ends with dark brown or black.

The ventrum is pinkish-cinnamon, especially centrally, with extensive irregular dark-brown blotching along the outer edges of the ventrals. There are six tail rings, the first four fawn, the last black; all are wider and darker dorsally. The rattle matrix is black. The tail is mottled below.

DESCRIPTION OF THE SUBSPECIES. — The paratypic series includes the following specimens: SDSNH 19717-8, 19990-5, 44358, 51991-3, 51995-6; CAS 50869-70, 50904; USNM 8562, 15978, 64588.* Together with the holotype, whose statistics are included in the following summary, there are 12 males and 9 females. There is also an unborn brood of 8 (SDSNH 44401-8), which are fully formed (except one defective) and with patterns already clearly in evidence. To avoid the effects of familial uniformity, I have not used the statistics of these juveniles except in blotch counts.

^{*}The USNM catalogue entry indicates uncertainty as to the origin of this specimen with the statement "doubtless from Cedros Island". But Townsend's field notes indicate that 64588 came from Ángel de la Guarda. Furthermore, extensive collecting on Cedros during the past 50 years has failed to produce another specimen of *C. mitchelli*, although many specimens of *C. essul* have been found there.

In presenting statistics and data on the paratypic series, and therefore of the new subspecies as now known, I shall at the same time point out the nature and extent of the differences that have been observed between *C. m. angelensis* and the other subspecies of *C. mitchelli*.

The new island form is certainly the largest of the *C. mitchelli* subspecies. Of the 21 specimens now available (excluding the brood), 5 reach or exceed 1240 mm. The longest is a male of 1367 mm. Of the two largest mainland subspecies, *m. mitchelli* and *m. pyrrhus*, only 9 out of 250 adults that I have examined measure 1000 mm. or more; the longest of these, a male from Escondido, San Diego County, is 1114 mm. In appearance, the new subspecies is even more striking than indicated by length alone: a 1367 mm. snake is nearly twice as bulky or heavy as one 1114 mm. long.

In C. m. angelensis the adult tail proportion of males averages 7.7 per cent, of females 5.7 per cent. The male proportion falls between those of m. mitchelli and m. pyrrhus; the female seems shorter than either (see Klauber 1956, table 4:3, p. 158). The new subspecies has a considerably larger head, proportionately, than m. mitchelli and slightly larger than that of m. pyrrhus (Klauber 1956, table 4:2, p. 154). The following figures represent the number of times the head is contained in the overall body length of a large male: m. mitchelli 27.0, pyrrhus, 23.0, angelensis 22.6. But at a body length of 1000 mm., which would be a fully grown pyrrhus but a still growing angelensis, the respective figures would be 23.0 and 21.0. This fact tends to validate a prior conclusion concerning head proportionalities in related groups (Klauber 1938, p. 20).

The rattle of *C. m. angelensis* in its early segments is peculiarly small. *Crotalus m. mitchelli*, although a rattlesnake of only moderate size, has the largest rattle button of any rattlesnake, even exceeding the buttons of such giants as *C. adamanteus* and *C. atrox.* Fortunately, I have available 5 specimens of *angelensis* with buttons; of these the dorso-ventral widths are 5.1 to 5.3 mm., mean 5.2 mm. The corresponding means of other *C. mitchelli* subspecies are: *mitchelli* 8.2, *pyrrhus* 6.7, *muertensis* 5.8, *stephensi* 5.1 (Klauber 1956, table 5:6, p. 289). The succeeding average increment in rattle width for each of the next 3 or 4 segments in *angelensis* is 1.1 mm., compared with 1.5 in *m. mitchelli*, 1.1 in *pyrrhus*, and 0.9 in *muertensis*. Thus *angelensis* never attains the rattle size of either *mitchelli* or *pyrrhus* until the snake has reached a body length which the mainland subspecies never attain.

The fangs of *angelensis* are relatively shorter than in the other subspecies; their length is contained in the head length about 7.6 times and in the length overall about 170 times (for the other subspecies see Klauber 1956, table 11:1, p. 736).

Data on the meristic characters of the paratypic series of *angelensis* are as follows: midbody scale rows 25 or 27 (6 out of 21 have 25 rows); ventrals (males) 180 to 187, mean 184.8 (females) 186 to 190, mean 188.2; subcaudals (males) 23 to 28, mean 25.4 (females) 19 to 21, mean 20.1; supralabials 12 to 15, mean 13.8; infralabials 13 to 17, mean 14.9; body blotches 36 to 46, mean 41.0; tail rings (males) 6 to 8, mean 6.9 (females) 4 to 6, mean 5.0. Comparisons with the other *C. mitchelli* subspecies may readily be made by consulting Klauber 1956, table 2:7, p. 124. *Crotalus m. angelensis* differs from the others to an important degree in four of these characters, as indicated in the following table:

	Scale rows	Ventrals (mean)		Body blotches
	(mode)	Males	Females	(mean)
C. m. angelensis	27	184.3	188.2	41.0
C. m. mitchelli	25	176.3	178.9	32.3
C. m. pyrrhus	25	178.0	178.7	33.3
C. m. muertensis	23	179.7	178.3	35.7
C. m. stephensi	23	174.3	179.0	36.8

Crotalus m. angelensis has the peculiarity in head scales that distinguishes C. mitchelli subspecies (except stephensi) from all other rattlesnakes, namely the almost universal separation of the rostral from the prenasals by other scales. This feature is found to an appreciable extent (about 17 per cent) in only one other form — Crotalus viridis cerberus, the black rattlesnake of Arizona. But C. m. angelensis differs from m. mitchelli and m. pyrrhus in usually having the interposed scale between each prenasal and the rostral in the form of a single scale of substantially the same height as the prenasal, whereas in the others the interposed scales are usually smaller. Prefoveals are more often in contact with the rostral in the two mainland forms, and the internasals are generally smaller. These differences are best indicated by the ranges and means of the total scales in contact with the rostral, as shown in the following statistics:

	Scales in contact with the rostral		
	Range	Mean	
C. m. angelensis	6-10	6.9	
C. m. mitchelli	7 — 11	9.5	
C. m. pyrrhus	5-11	7.7	
C. m. muertensis	6-10	8.4	

Probably the most consistent key character wherewith to segregate angelensis from either *m. mitchelli* or *pyrrhus* is the presence of sutures or other blemishes in the supraoculars. These are extensively present in *stephensi* and *muertensis*, but we need not rely on the supraocular sutures to key out these two: the prenasal-rostral contact in *stephensi* and its absence in *angelensis*, will segregate *stephensi*; and scale rows and body size will differentiate *muertensis*. But supraocular sutures are important in distinguishing the other two subspecies; for they occur in only 3 per cent of *m. mitchelli*, about 10 per cent of *pyrrhus*, and 95 per cent of *angelensis*. They are not so obvious in *angelensis* as in *stephensi*; nevertheless they are nearly always present, particularly as seams indenting or parallel with the outer edges of the supraoculars.

In color and pattern, *C. mitchelli* is the most variable of all rattlesnakes, with the single exception of *C. viridis*, which is found throughout a much larger and ecologically more variable area. Some local color phases of *C. m. pyrrhus* are particularly striking: the burnt-orange colored specimens of the Santa Ana mountains of southern California, the coral pink or red snakes of some parts of central Arizona, and the cream-colored snakes of the Tinajas Altas range, a southerly continuation of the Gila Mountains in extreme southern Arizona.

Crotalus m. angelensis shows considerable uniformity in color but no special brilliance. It begins life as a gray snake with dark gray hexagonal blotches, and then changes gradually through tan or buff with brown blotches to an eventual pink with russet blotches when fully adult. The blotches do not have the even outlines or light borders characteristic of so many rattlers; they are produced by a darker ground color with increased stippling. There is a smaller, secondary series of blotches on either side; with these the posterior dorsal blotches merge to form crossbands. In almost all specimens, some anterior scales of the blotches are tipped posteriorly with dark brown or black; these are more prevalent in angelensis than in other mitchelli subspecies.

The ventrum in adults is pinkish-cinnamon, especially midventrally, with irregular brown blotching on the outer edges of the ventral scutes.

The head is colored similarly to the body. The darker blotches are variable and indistinct. Ventrally, the head is cream colored. The side stripes characteristic of the heads of most rattlesnakes, if present at all, are quite inconspicuous. Very young snakes have a light supraocular crossdash widening inwardly, but this disappears at an early age.

The anterior tail rings are of the same color as the body and are largely composed of punctations. The last two or three rings are black. The rings narrow laterally and become less distinct ventrally. The rattle matrix is black.



FIG. 2. Allan Kuebler and Chris Parrish with Ángel de la Guarda Island Speckled Rattlesnakes which they collected at Arroyo Estatón, Ángel de la Guarda Island, April 22, 1960. Photograph by George Lindsay.

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In the more important characters that distinguish *pyrrhus* from *m. mitchelli*, such as head size, rattle width, and the nature of the separation between the rostral and prenasal, *angelensis* is shown to be more closely allied to *pyrrhus* than to *m. mitchelli*, just as would be expected from territorial considerations, for Angel de la Guarda lies off the part of the peninsula occupied by *pyrrhus*. A rather frequent occurrence of elongated final supralabials in *angelensis* is the only character suggesting a closer relationship with *m. mitchelli* than with *pyrrhus*.

The occurrence of the largest subspecies of *C. mitchelli* on an island is contrary to the usual relationships between insular forms of *Crotalus* and their nearest mainland relatives; for the insular forms generally are smaller. In each of the following pairs, for example, the insular form (named first) is smaller: *C. tortugensis* and *C. atrox*, *C. exsul* and *C. ruber ruber*, *C. catalinensis* and *C. scutulatus scutulatus*, *C. molossus estebanensis* and *C. m. molossus*, *C. unicolor* and *C. durissus terrificus*, *C. viridis caliginis* and *C. v. helleri*, and *C. mitchelli muertensis* and *C. m. pyrrhus*. (Not enough specimens of *C. enyo cerralvensis* are available to determine its size relationship with *C. e. enyo*.) Of all the pairs mentioned above, the size relationship of *C. m. muertensis* to *C. m. pyrrhus* is most in contrast with that of *C. m. angelensis* to *C. m. pyrrhus*: whereas *angelensis* is larger than *pyrrhus*, *muertensis* is a stunted form about 60 per cent of the length of *pyrrhus*. Yet *muertensis* also occurs on an island (El Muerto) off Baja California, and only about 75 miles from Ángel de la Guarda.

Why C. m. angelensis should reverse the usual trend of island forms in rattlesnakes (and other genera as well — Klauber 1956, p. 304) is not known. Angel de la Guarda is a large island, with a length of 48 miles and a maximum width of 12 miles. Ecologically, it is favorable to rattlesnakes, with good cover and a plentiful food supply, of both small mammals and lizards. Yet C. ruber ruber, also found on the island, though not so plentiful as angelensis, does not reach so large a size as ruber on the adjacent peninsula, although it is not conspicuously stunted.

It should not be assumed, from the number of island subspecies mentioned, that subspecific differentiation is a normal or invariable result of island colonization by rattlesnakes. On the contrary, in the Gulf of California alone, besides the pairs already mentioned, no less than 7 species of rattlers are found on 14 other islands without subspecific differentiation having become evident, at least so far as can be determined from the available material. Among these there are 5 other islands inhabited by C. m. mitchelli.

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