RESULTS OF THE PURITAN-AMERICAN MUSEUM OF NATURAL HISTORY EXPEDITION TO WESTERN MEXICO

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RICHARD G. ZWEIFEL

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INTRODUCTION

ONE OF THE PRINCIPAL OBJECTIVES of the Puritan-American Museum expedition of 1957 (Emerson, 1958) was the collection and study of reptiles and amphibians of the islands of western Mexico. The Tres Marías Islands were accorded special attention, as studies of previous workers indicated that the vertebrate fauna is largely endemic, and hence of considerable significance to the study of evolution on islands. The geographic position of the Tres Marías Islands also contributes to their interest, as these are the only islands of any significant size on the tropical Pacific coast of Mexico.

The "Puritan" spent the period from March 23 to April 7, 1957, at the Tres Marías Islands. Details of the time spent on the different islands are given in a following section in which the islands are described. The highly varied collecting activities together with time spent in making contact with local officials and in inter-island travel somewhat restricted the period available for collecting reptiles and amphibians. Nevertheless, the herpetological collections contain most of the species previously recorded for the islands as well as others formerly not known to be present.

The purpose of this paper is to present an analysis of the herpetofauna of the Tres Marías Islands, stressing the comparison of insular and mainland populations and emphasizing the geographic relationships of the herpetofauna.

ACKNOWLEDGMENTS

The members of the scientific party aboard the "Puritan" at the time of the visit to the Tres Marías included Dr. William K. Emerson, Dr. Richard G. Van Gelder, and Mr. Oakes Ames Plimpton, in addition to the author. All participated in collecting activities, and I wish to express my thanks to the other members of the scientific party and to the crew of the "Puritan" for their aid. A special word of thanks is reserved for Mr. Harry J. Bauer, whose initiative, interest, and support made the expedition possible.

A number of persons contributed generously in various ways to further this study. Señor Alfonso R. Benavides, a temporary resident of María Madre Island, not only provided assistance in the field, but forwarded to the American Museum a small collection of reptiles and amphibians made after the departure of the "Puritan." Mr. Robert L. Fisher of the Scripps Institution of Oceanography furnished a recently completed map of sea bottom topography of western Mexico. Dr. Norman Hartweg and Dr. Hobart M. Smith examined and identified reptile specimens from the Tres Marías, and Dr. Manning A. Price, Agricultural and Mechanical College of Texas, identified ticks removed from snakes in the collection. Lists of specimens appropriate to this study were furnished by Dr. L. M. Klauber, Dr. Alan Leviton, and Dr. Charles F. Walker. Dr. Kenneth E. Stager donated a small collection of reptiles from the Tres Marías, and helped with his personal knowledge of the Tres Marías Islands.

I wish to express my appreciation to Mr. Charles M. Bogert, who read this paper in manuscript and made many valuable suggestions, and to Dr. Norman D. Newell for advice on geological matters.

This paper is based largely on the collections made on the Puritan-American Museum expedition and deposited in the American Museum of Natural History, but specimens in other museums have been consulted as well. I am grateful for the loan of specimens, or permission to examine material in these museums. Abbreviations used in this paper are listed below:

A.M.N.H., the American Museum of Natural History, New York
C.A.S., California Academy of Sciences, San Francisco
S.D.S.N.H., San Diego Society of Natural History, San Diego
U.M.M.Z., University of Michigan Museum of Zoölogy, Ann Arbor
U.S.N.M., United States National Museum, Washington

DESCRIPTION OF THE TRES MARÍAS ISLANDS

The Tres Marías are a chain of four islands oriented along a line trending northwest from the vicinity of Banderas Bay at the border of the Mexican states of Jalisco and Nayarit (fig. 1). The point of land nearest the islands is Punta Mita on the northern edge of Banderas Bay, approximately 50 miles from María Cleofas Island. Progressively along the chain, the islands (and their approximate distances from Punta Mita) are María Magdalena (65 miles), María Madre (80 miles), and San Juanito (95 miles). San Juanito Island is farthest offshore, about 70 miles from the mainland. There is scant knowledge of the geography of the Tres Marías Islands, and there are no maps showing the individual islands in detail. Even the position of the chain of islands is not well established, as witnessed by the following statement from the "Sailing Directions" (United States Navy Hydrographic Office, 1951, p. 134): "Las Tres Marías Islands have been reported to be charted 3 miles westward of their true position, and a recent report places the 1,320-foot peak of Cleopha Island . . . approximately 3 miles northward of its present charted position." An attempt to secure aerial photographs of the islands met with the response from Mexican officials that the photographs are regarded as confidential, and their use was restricted.

As is shown in figure 1, the sea bottom slopes gradually out from the mainland opposite the Tres Marías to a depth of over 200 fathoms, and then rises abruptly to the islands. On the seaward side, the bottom falls off precipitously to as much as 2300 fathoms. A submerged peak with a minimum depth of only 35 fathoms is situated between María Cleofas and Punta Mita. A deep submarine canyon occupies Banderas Bay, and a suggestion of a similar feature is seen between Punta Mita and the submerged peak.

Brief notes on the individual islands and the collecting activities of the party follow.

San Juanito Island

This is the smallest and northernmost of the four islands that constitute the Tres Marías Group, and is separated from María Madre Island by a shallow channel about 2 miles in width. It is stated in the "Sailing Directions" (United States Navy Hydrographic Office, 1951, p. 135) that San Juanito Island "has a length of $2\frac{1}{2}$ miles, a maximum width of $1\frac{1}{4}$ miles, and a height of about 150 feet, at its northern end, whence it slopes gradually to the southward." Nelson (1899, p. 10) credits the island with being "3 or 4 miles in diameter and about 100 feet high," and Stager (1957, p. 414) gives the dimensions of the island as "4 miles long and 3 miles wide." The confusion reflects the poor state of knowledge of the geography of the Tres Marías Islands. Converted to statute miles, the Hydrographic Office figures are approximately 2.9 by 1.4 miles.

The elevated (though largely level) surface of the island away from the beach is covered by a dense growth of low trees, brush, and agaves with an average height of about 10 feet (pl. 42). Occasional trees project above this level. The sisal growing here is harvested by convicts from María Madre, and a network of roads has been made to facilitate this activity. Were it not for these roads, penetration to the interior of the island would be difficult, if not impossible, such is the density of the vegetation. There appears to be no fresh water on the island, though a cistern at some dilapidated shacks on the beach held what may have been rain or tidal water. Herpetological collecting was carried on for only half of a day, the morning of March 27.

María Madre Island

María Madre is the largest of the Tres Marías Islands, and is "nearly 12 miles [13.8 statute miles] long and 3 to 6 miles [3.5 to 7.0 statute miles] wide. The highest peak, near the center of the island, is 2020 feet high, but the peak that lies about midway of the southwestern side of the island is the most prominent" (United States Navy Hydrographic Office, 1951, p. 135). Collecting parties from the "Puritan" were ashore on María Madre on March 24, 25, and 26, and on April 5, 6, and 7.

The Government of Mexico maintains a penal colony on María Madre, and at the

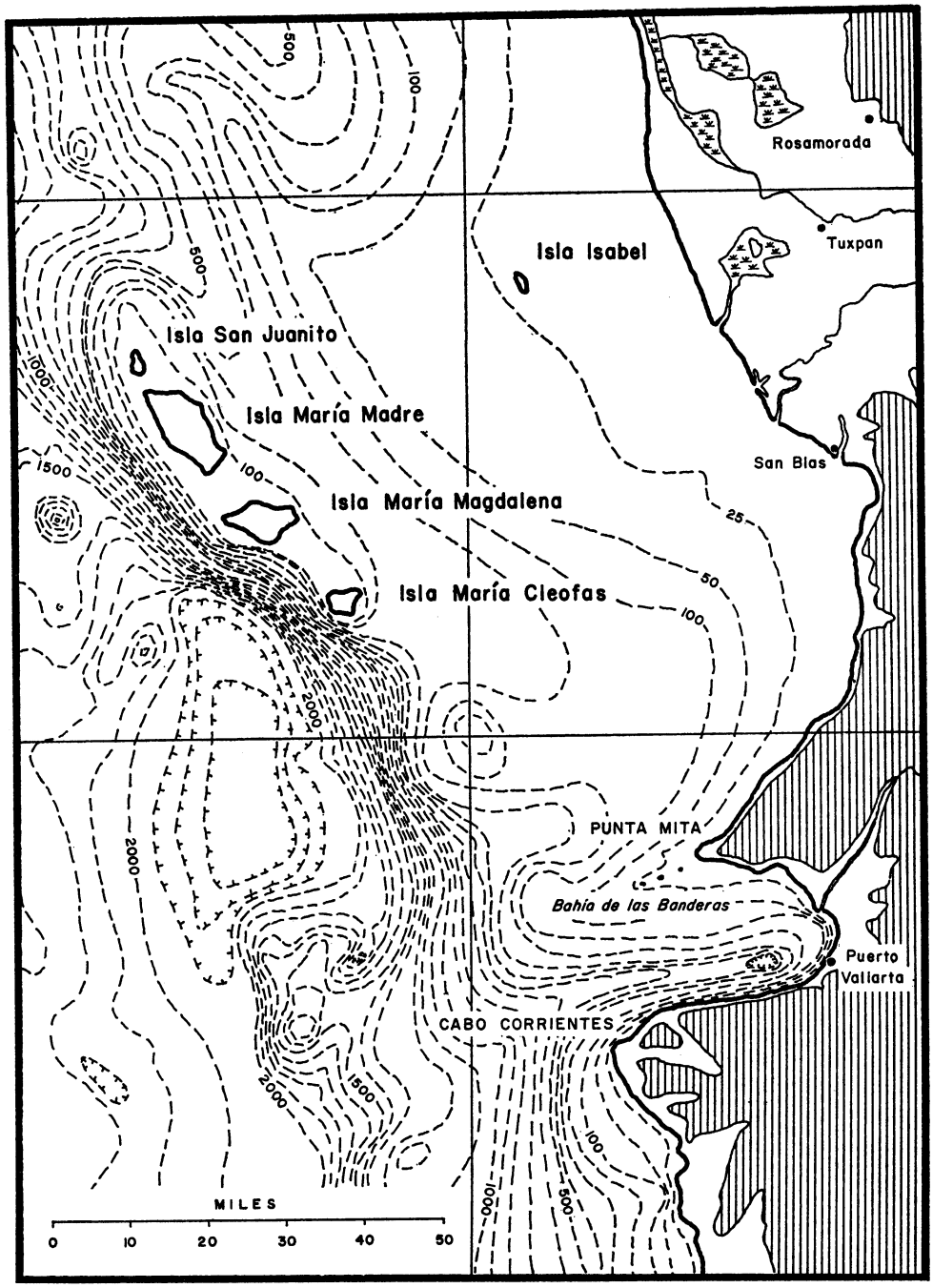


FIG. 1. The Tres Marías Islands and adjacent mainland. Submarine contour interval is 100 fathoms, with 25- and 50-fathom contours added; contours adapted from an unpublished map furnished by Robert I. Fisher. Areas on the mainland above the 300-foot contour are indicated by shading, marking approximately the division between coastal plain and foothills; similar elevations on islands are not shaded. For the position of the islands in relation to a greater area of the mainland, see figure 3.

time of our visit the inhabitants of the island numbered about 700 convicts and 100 soldiers. The status of the island as a penal colony somewhat limited our collecting activities (for example, we worked on the island only during daylight hours), but, with the cooperation of government officials, we were able to arrange transportation by truck, and permission was granted for several convicts to serve as guides and collectors.

In the more or less level coastal region about the settlement on the eastern side of the island the vegetation, where not altered by human activity, is low Tropical Deciduous Forest with a canopy height of 10 to 12 feet. In the midst of the dry season, there was little sign of life in the vegetation, with agaves and giant columnar cacti providing almost the only greenery. The interior of María Madre Island is forested, though lumbering evidently has brought about considerable change in the vegetation. Nelson (1899, p. 12), writing of the conditions at the time of his visit in 1897, says: "In its primeval condition, before the advent of the woodcutters, it must have presented a fine example of tropical forest growth. Now, only a few specimens remain to show what the original condition must have been." Driving to Arroyo Hondo at the northern end of the island, we noted the stature of the forest to increase considerably as one moves inland to higher elevation. The largest trees are over 100 feet in height but are nowhere numerous enough to form an important part of the canopy.

On March 25 and again on April 7 parties from the "Puritan" visited Arroyo Hondo, a canyon at the northern end of the island with its mouth approximately 6 miles from the main village.

Probably because of the presence of surface and subsurface water, the vegetation of Arroyo Hondo was considerably greener than any seen elsewhere on the island. Numerous large trees, including gigantic figs, were present (pl. 41). Water, a rarity during the dry season in the Tres Marías, is the main feature of interest in this canyon. At the time of our visit, water was found along about one-half of a mile from the canyon, though in a few places along this stretch there was no surface flow. The stream was nowhere more than 2 or 3 feet wide and a few inches deep. A few small pools of greater dimensions were present, the largest of which measured about 7 feet by 4 feet, by 16 inches deep. A *Kinosternon* was found in this pool, but no other sign of aquatic vertebrates (fish, amphibian, or reptile) was seen. The frogs found here (*Syrrhophus*) are not aquatic but occur under shelter in moist places near the stream. Collecting along the stream was difficult, as almost all the stream had been covered with cut brush by convicts. This was done to deny birds access to the stream, forcing them to seek water at the few remaining open spots. Box traps operated by a string from a nearby blind were used to capture the desired birds (doves) which were used as food by the trapper or sold to other convicts to supplement a somewhat drab diet. Arroyo Hondo was visited by Hanna (1926, p. 71) who noted that at the time of his visit (May 17) running water was present for only about 100 feet.

In addition to the time spent in Arroyo Hondo, some collecting was done in the vicinity of the main village and in the low forest inland from the salt works about 4 miles south of the village. The remaining time ashore was devoted to establishing contacts with officials and convicts and to purchasing specimens.

María Magdalena Island

María Magdalena is the second largest of the Tres Marías, after María Madre, and is situated to the southeast of that island, separated from it by a channel said to be 4 nautical miles (4.6 statute miles) in width. According to the "Sailing Directions" (United States Navy Hydrographic Office, 1951, p. 134), the island has maximum dimensions of 8 miles (9.6 statute miles) from east to west and 4.5 miles (5.2 statute miles) north to south. The maximum elevation is given as 1500 feet.

The forest on María Magdalena is evidently less disturbed than that of María Madre. Nelson (1899, p. 12) records that "On María Magdalena the conditions were similar to those on María Madre, but a larger percentage of the original forest still

remains intact," and 58 years later Stager (1957, p. 415) is still able to write that "the original plant cover has not been altered to any noticeable degree." The vegetation of the north side of the island is described briefly in my field notes as follows: "Clumps of low, spiny grass along the edge of the beach quickly give way to dense scrub 8 to 10 feet high a short distance inland. The forest is 20–30 feet high in level regions, but as one passes up the arroyos, much taller trees become common, and hundred-footers are not rare. Bromeliads are common in the low forest, and hanging and climbing vines (mostly dry at this time of the year) are abundant everywhere. Away from the vicinity of the beach there is almost nothing in the way of herbs, and shrubs are infrequent and picked clean by the deer and goats." The observations concerning the impact of introduced deer and goats on the vegetation are at variance with those of Stager (*loc. cit.*), who states that "the goats do not seem to have caused any appreciable damage by their browsing." The more abundant green shrubs on María Cleofas Island (see account on p. 88), where there are no deer or goats present, would seem to suggest either a fundamental difference in the vegetation or, as seems more likely, a distinct inhibitory effect of the herbivores on the plants. This effect is most plain during the dry season, and differences would probably be much less evident during the summer growing season.

Collecting parties from the "Puritan" went ashore on María Magdalena at three points: on March 28, at "Gringo Bay" on the southwestern side of the island; on March 29 and 30 on the southeastern side of the island; and on March 31 to April 2 near a lagoon on the north side of the island.

The stop at "Gringo Bay" was a brief one of about three hours in the morning. Little collecting was done, and the "Puritan" moved to a more favorable anchorage on the southeastern side of the island.

Collecting on March 29 on the southeastern side of the island was concentrated along a drainageway that follows a sinuous path for about 1 mile through the forest. At the head of this dry creek bed at an elevation of 100 feet (by altimeter) surface water was found. The locality is of interest as one of the places where *Syrrhophus* was collected. A *Boa* was also captured here, and *Phyllodactylus*, *Anolis*, *Ctenosaura*, and *Cnemidophorus* were found in the same general vicinity. A description extracted from my field notes characterizes the habitat as follows: "An arroyo in Tropical Deciduous Forest. The arroyo at this point is about 25 feet wide and cut down about 6 feet from slightly sloping land on one side and more abrupt slopes on the other. The bottom is composed of earth (not sand) with numerous rocks up to 2 feet in diameter. . . . The surface water is confined to about 100 feet of the arroyo—I covered the stream bed from mouth to divide. The water is in a series of pools 2 to 3 feet in diameter, 4 or 5 inches deep, and . . . largely choked with leaves. There is no discernible surface flow between pools except those closely adjacent, only muddy stretches with wet leaves. Water temperatures in two pools were 21.4° and 19.6° C., air at 3 feet at 14:10, 26.6° C. There is an almost complete canopy of tall trees up to or over 70 feet in height over this part of the arroyo. At midday, only scattered patches of direct sunlight reach the bottom of the stream bed. There is a cover of dry leaves in the arroyo bottom, but no vegetation there." This locality was revisited on the evening of March 30, but no additional frogs were found. At night, land crabs were the most conspicuous element of the fauna.

On March 31, the "Puritan" moved to an anchorage on the north side of María Magdalena Island. We had been advised that water could be found by following a foot trail inland from a pair of dilapidated shacks on the beach opposite our anchorage. The trail indicated was found without difficulty, and after a walk of about 15 minutes' duration, a small tributary arroyo, which held surface water for a distance of about 100 yards, was found. Occasional small, shallow pools were present, but for the most part the stream bed had been trampled into a muddy mass by the deer and goats. A short walk up the main drainage, the canyon narrowed, and water was again encountered. Here the canyon was narrow and rocky, and the water in pools was up to 1 foot in depth, with some flow between pools. The arroyo ended abruptly against a nearly verti-

cal cliff about 60 feet in height. A slight trickle of water moistened the cliff face and provided for an abundant growth of moss and ferns. *Syrrhophus* was found near the water in both the main and tributary arroyos. Snakes found closely associated with the water were *Boa*, *Dryadophis*, and *Drymarchon*. Work in the canyon was resumed on the morning and evening of April 1. No nocturnal frog activity was detected, and even the crabs, so abundant at the water at a lower elevation on the southeastern side of the island, were absent.

María Cleofas Island

María Cleofas Island is the southernmost island of the Tres Marías, and is separated from María Magdalena by a channel approximately 9.8 miles in width. The island "is nearly circular in form, with a diameter of about 3 miles [3.4 statute miles]. The highest peak has an altitude of 1,320 feet" (United States Navy Hydrographic Office, 1951, p. 134). The "Puritan" anchored off the east coast of the island on the afternoon of April 2, and collecting parties were ashore for a short time on that day as well as on the two following days.

Stager (1957, pp. 415–416) has corrected Nelson's (1899, p. 12) erroneous description of the vegetation of María Cleofas, which was said to be rocky and sterile, with the trees stunted and brushy. Stager states: "María Cleofas has a vegetative cover which is almost intact . . . our investigations revealed dense forests on the slopes and level land on the eastern side of the island." A brief summary of the vegetation as observed on the eastern side of the island is recorded in my field notes: "The vegetation immediately behind the beach is an almost impenetrable tangle of vines, thorny shrubs, cactus, and agaves. The height is about 8 feet, with an occasional giant cactus, covered with vines, protruding another few feet. Fifty to 100 yards behind the beach the vegetation opens up slightly into low forest, with trees about 30 feet tall and a layer of terrestrial bromeliads disposed in thickets beneath. As the height of the canopy increases, the bromeliads disappear and are replaced by cycads [see Stager, 1957, pl. 20] of about the same height (3–4 feet). . . . There are few really large trees, but I estimate a 70-foot canopy is maintained over a considerable area. Notwithstanding the dry conditions, there are considerable green shrubbery and vines in the understory." The difference in the understory vegetation between this island and María Magdalena may be attributable, in part at least, to the presence of deer and goats on María Magdalena (see p. 87).

According to the "Sailing Directions" (United States Navy Hydrographic Office, 1951, p. 134), there is a fresh-water spring about 70 yards south of the lagoon at which we landed on the eastern side of the island, and Nelson (1899, p. 10) mentions the presence of a little stream on María Cleofas, where fresh-water fish occur. However, we were unable in the short time available to find any surface water on the island.

CLIMATE OF THE TRES MARÍAS ISLANDS

Climatic data for the Tres Marías Islands, specifically for a station on María Madre (presumably at Puerto Balleto), are given by Contreras (1942, p. 29), and are shown graphically in figure 2. The average yearly rainfall is 635 mm., or about 25 inches. Most of this comes in the summer, with the greatest amount (191 mm.) in September. Little or no rain falls in the late winter and spring; a small amount falls in June, building up to the late summer peak. The summer rains sometimes accompany violent storms (*chubascos*), and hurricanes sweep up the coast from the southeast, most frequently in September and October (Roden, 1958, p. 29, fig. 6).

The most interesting feature of the climate of the Tres Marías is the aridity, compared to nearby points on the mainland. Cabo Corrientes, southeast of the islands, receives 952 mm. (37.5 inches) annually, and Puerto Vallarta 1484 mm. (58 inches). San Blas,

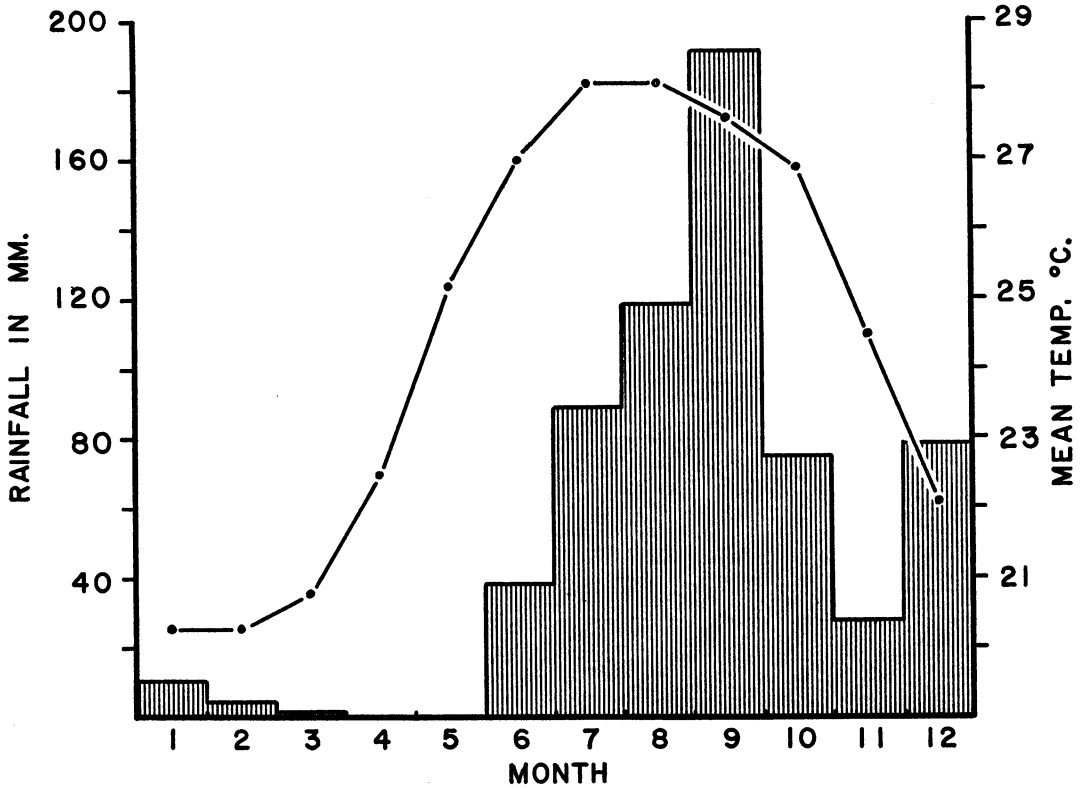


FIG. 2. Climate of the Tres Marías Islands. Shaded bars indicate the mean monthly rainfall; the line connects points designating mean monthly temperature.

directly east of María Madre, averages 1462 mm. (57 inches) per year. Among the several west coast stations tabulated by Contreras (*supra cit.*), the one most similar to from the southeast, most frequently in Sep- María Madre is Culiacán, Sinaloa, which receives 605 mm. (24 inches). Culiacán is on the coastal plain about 220 miles north of the Tres Marías and is situated in a region dominated by Thorn Forest. This vegetation contrasts markedly to the high Tropical Deciduous Forest of the Tres Marías; the presence of this forest suggests that the rainfall records may give a somewhat erroneous impression of aridity on the islands. Presumably the records are taken at the prison colony on the east side of the island, as this is the administrative center. There may be a rain-shadow effect on the landward side of the island, behind the 2000-foot peaks.

Temperature fluctuations on the islands are moderate, undoubtedly owing to the influence of the ocean. The monthly averages range from 20.3° C. (68.5° F.) in January and February to 28.1° C. (82.6° F.) in July and August. Freezing temperatures are unknown, with the recorded extremes being 4.6° C. (40.3° F.) and 37.5° C. (99.5° F.). The monthly average temperatures are similar to those at San Blas, being less than 1° C. above the corresponding figures for San Blas. The winter and spring months are slightly warmer at Cabo Corrientes and Puerto Vallarta, but summer temperatures are nearly identical with those of the islands. Both minimum and maximum temperatures are higher at these two localities than on María Madre: the range 12°–43.8° C. (53°–110.8° F.) at Cabo Corrientes, and 9.5°–39° C. (14.1°–102.2° F.) at Puerto Vallarta.

HISTORY OF HERPETOLOGICAL COLLECTING ON THE TRES MARÍAS ISLANDS

Apparently the first naturalist to take note of the reptile life of the Tres Marías Islands was the ornithologist Andrew Jackson Grayson, who visited the islands in 1865, 1866, and 1867. Notes by Grayson on the geography and natural history of the islands were edited by George N. Lawrence and published (Grayson, 1871) after Grayson's death in 1869 of a fever contracted on Isabel Island. While the detailed accounts in the paper pertain to birds, Grayson notes that "Among reptiles, there are two or three species of *tree* snakes, and the Mexican anaconda is sometimes met with. Various species of lizards are abundant, among which a very long one, two feet in length, known as the iguana, is very common." Except for the mention of several dates in January, 1865, Grayson does not record how much time was spent on the islands, or what time of year he was there. Apparently no herpetological specimens were collected. Alfred Russel Wallace (1876, pp. 59–60) used Grayson's record of several species of lizards and snakes as evidence for the continental nature of the Tres Marías Islands, and referred to the "Mexican anaconda" more correctly as the boa constrictor.

Probably the first herpetological collections to be made on the Tres Marías, certainly the first of any significance, were those made by Alphonse Forrer for Godman and Salvin and deposited in the British Museum (Natural History). There appears to be no published record of the amount of time Forrer spent on the islands, though the dates March 10 and April 23, 1881, accompany accounts of mammals from the islands in the "Biologia Centrali-Americana." Godman (1915, p. 19) merely states that "Alphonse Forrer collected in María Madre on our [Godman's and Salvin's] behalf and obtained a large number of specimens." Although Godman specifically mentioned María Madre Island, all records of reptile specimens collected by Forrer have been cited "Tres Marías Islands," not only in the "Biologia Centrali-Americana," but in Boulenger's catalogues as well. The collection made by Forrer was never reported on as a unit, but from the accounts in Boulenger's catalogues of snakes (1893–1896), lizards (1885–1887), and chelonians (1889), it appears that 43 specimens were gathered: 21 snakes of eight species; 20 lizards of five species; and two turtles of the single species known on the islands. Most of these specimens were dealt with in the "Biologia Centrali-Americana" (Günther, 1885–1902).

Under the auspices of the Division of Biological Survey, United States Department of Agriculture, E. W. Nelson and E. A. Goldman worked on the Tres Marías for most of the month of May, 1897, collecting a wide variety of zoological and botanical specimens. Over half of their time was given to María Madre, and only short periods were spent on the other three islands (Nelson, 1899). The reptile specimens (as detailed by Stejneger, 1899) numbered 69, including 14 snakes of seven species, 50 lizards of five species, and five specimens of the single species of turtle. The collection largely duplicated that of Forrer in terms of species obtained, including only one species he missed, *Boa constrictor*, but lacked two that Forrer had captured, *Leptophis diplotropis* and *Imantodes gemmistratus*.

In May, 1925, an expedition from the California Academy of Sciences visited the Tres Marías. Joseph R. Slevin, at that time Assistant Curator of Amphibians and Reptiles in the Academy, accompanied the expedition. Collecting was carried on for seven days on María Madre and three days on María Magdalena. San Juanito and María Cleofas were not visited. Hanna (1926) gave a general account of the expedition, and Slevin (1926) described the herpetological collections. The reptile specimens collected total 398. [A list of the number of specimens collected, information not contained in Slevin's paper (1926), was kindly furnished by Dr. Alan Leviton.] Of these, 12 are snakes, one is a turtle, and the remaining 385 are lizards. Specimens of the lizards and turtles previously known were obtained, but some snakes taken by the previous expeditions were not found. These were *Lampropeltis*, *Lep-*

tophis, *Imantodes*, and *Agkistrodon*. Added to the fauna of the islands were the snakes *Exelencophis nelsoni* (described as a new species, *Tantilla nelsoni*) and *Pelamis platurus*.

No major collection was made on the Tres Marías subsequent to the California Academy of Sciences Expedition of 1926 until the visit of the "Puritan" nearly 31 years later. Herpetological specimens collected included 41 anurans, three turtles, 99 lizards, and 30 snakes. The snakes *Imantodes*, *Exelencophis*, *Agkistrodon* and *Pelamis* collected on previous expeditions were not found by members of the Puritan expedition. Species added to the fauna of the islands include the first amphibians to be recorded, *Syrrhophus modestus* and *Bufo mazatlanensis*, and the snake *Tantilla calamarina*. All other species of reptiles known to occur on the islands were collected.

The collections made by Forrer, Nelson, and Goldman, the California Academy of Sciences expedition, and the Puritan-American Museum expedition contain the bulk of specimens taken on the islands. A few specimens collected at other times are deposited in various museums. Kenneth Stager collected reptiles while engaged in an ornithological survey (Stager, 1957) and deposited these in the American Museum. William H. Burt collected reptiles on María Magdalena and María Cleofas that are in the collection of the University of Michigan Museum of Zoölogy. Others have been deposited in the San Diego Museum of Natural History, the collection of Dr. L. M. Klauber, and the Stanford University Museum of Natural History.

KEY TO THE AMPHIBIANS AND REPTILES OF THE TRES MARÍAS ISLANDS

The species of reptiles and amphibians inhabiting the Tres Marías Islands are sufficiently distinct from one another that a herpetologist with knowledge of the American fauna and the list of insular forms on hand will have little difficulty in identifying the species on first sight. The possibility exists that other biologists while in the field may wish to identify species of the Tres Marías fauna. With their needs in mind, I have prepared the following artificial key. Characters in addition to the bare minimum necessary for identification are included, so that species new to the fauna may be recognized by their disagreement with the key. Marine reptiles and those major groups represented by only a single form (i.e., crocodile and turtle) are omitted.

Frogs

1. Size large, reaching a snout–vent length of over 3 inches; head with dark crests; skin rugose, warty; a pale, vertebral stripe; hind feet partly webbed . . . . . *Bufo mazatlanensis*

   Size small, maximum length about 1 inch; no crests, warts, or vertebral stripe; dorsal surfaces golden brown, with irregular markings; hind feet not webbed . . . . . *Syrrhophus modestus pallidus*

Lizards

1. Tail with whorls of enlarged, spiny scales separated by whorls of smaller scales; a denticulated vertebral crest, best developed in large males; size large, up to 3 feet or more in length; color variable, bright green or brown in young, reddish brown to black mottled with cream in adults . . . . . *Ctenosaura pectinata*

   Small lizards (under 2 feet in total length), tail without whorls of enlarged, spiny scales separated by whorls of smaller scales . . 2

2. Dorsal scutellation of body composed of tiny granules, with occasional larger tubercles interspersed; pupil vertical; distal portion of *unregenerated* tail ringed with black and white . . . . . *Phyllodactylus lanei*

   Dorsal scutellation of body uniform or with enlarged scales in middorsal region, not scattered; pupil not vertical; color of tail not in conspicuous rings 3

3. Dorsal scutellation of body composed of tiny, uniform granules, changing abruptly to whorls of larger scales on the tail; ventral surface of body with several rows of enlarged scales; young lizards dark brown with pale stripes, tail orange-brown; stripes vanish in largest individuals, which have dark blotches laterally and pale spots on rump . . . . . *Cnemidophorus communis mariarum*

Dorsal scutellation of body not uniform, middorsal scales gradually or abruptly enlarged, but distinctly larger than scales of lateral body wall; ventral scales smaller or no larger than middorsals; never a pattern of pale stripes on a dark background . . 4

4. Middorsal rows of scales conspicuously and abruptly larger than laterals; no throat fan; male with blue patches on abdomen and blue (possibly sometimes yellow) throat patch; digits unspecialized . . . . . *Urosaurus ornatus lateralis*

Middorsal rows of scales larger than laterals, but with gradual transition; male with a yellow, orange, and white throat fan; digits with expanded segment . *Anolis nebulosus*

Snakes

1. Pattern of dark and light rings 2

Pattern unicolored, blotched or striped but not ringed 3

2. Snout black; body with black and white rings (no red) . . . . . *Exelencophis nelsoni*

Snout yellow; body with black, white, and red rings . *Lampropeltis triangulum schmidti*

3. Head broad, with two prominent white lines on side, one running from tip of snout through upper edge of orbit, other from tip of snout along upper lip; heavy body; young individuals brown, with darker cross bands, darkening ground color in adults obscures pattern . *Agkistrodon bilineatus bilineatus*

Side of head not marked with two prominent white lines 4

4. Predominant color (in life) green; a dark stripe on the side of head and neck is interrupted before it disappears posteriorly . . . . . *Leptophis diplotropis*

Not green in life with a dark anterior, lateral stripe 5

5. Top of head without enlarged plates—only numerous small scales present . . . . . *Boa constrictor imperator*

Top of head covered with several large plates 6

6. Pattern of dark cross bands or blotches along length of body 7

Blotches, if present, restricted to neck region 8

7. Body exceedingly slender; head small and blunt, quite distinct from neck; pupil vertical; chin immaculate . . . . . *Imantodes gemmistratus gracillimus*

Head elongate; pupil round; chin spotted with dark brown or black . . . . . *Dryadophis melanolomus slevini*[1]

8. Small (under 1 foot long), secretive snake; gray or brown, with darker middorsal and lateral lines . . . . *Tantilla calamarina*

Larger species, all except hatchlings over 1 foot in length; pattern various, but never with distinct vertebral and lateral lines . 9

9. Adults uniform black or very dark blue; throat white or reddish; juveniles largely dark, but with light scales forming obscure cross bands . *Drymarchon corais rubidus*

Color not uniform black or largely black . 10

10. Chin shields and anterior abdominal scales with prominent dark markings; dorsal scales edged with black anteriorly, the pattern most evident when scales are spread; a dark line running along side of head from snout through eye, obscure or absent in adults . . . . . *Dryadophis melanolomus slevini*

Chin and anterior abdominal scales immaculate, or with indistinct marks on chin; dorsal scales immaculate or marked with black; dark line on side of head present or absent 11

11. A dark line running from tip of elongate, pointed snout, through eye (line may be obscure in darker individuals); body with little pattern other than in some individuals a black scale edge; upper lip pale, contrasting with darker sides of head above lip . . . . . *Oxybelis aeneus auratus*

No trace of a dark line along side of head; each dorsal scale with a black spot at tip and base, that at tip most evident; upper lip usually mottled, not abruptly differentiated from side of head above lip . . . . . *Masticophis lineatus*

[1] Juveniles only key out here; adults at couplet 10.

ACCOUNTS OF SPECIES

THE SYNONYMY FOR EACH SPECIES includes a reference to the original description of the form in question and references to the various names since applied to the insular population. I have included all references encountered, with the exception of the most trivial, so that the bibliography provides a fairly exhaustive list of writings on the herpetology of the Tres Marías Islands. The synonymies do not cover the literature for mainland populations.

Specimens collected on the Puritan-American Museum expedition are listed by island and museum catalogue number in separate paragraphs in each account. Where specimens from other sources have been examined, these are noted in the body of the text. A list of the reptiles and amphibians of the islands, giving their known distribution among the islands, comprises table 2.

Bufo mazatlanensis Taylor

Plate 43, figure 1

Bufo mazatlanensis TAYLOR, "1939" [1940], Univ. Kansas Sci. Bull., vol. 26, p. 492, type locality 2 miles east of Mazatlán, Sinaloa, Mexico.

María Madre Island (A.M.N.H. Nos. 60658–60661).

A southern population of this toad was described by Taylor (1943) as *Bufo nayaritensis*. Langebartel and Smith (1954) suggest that this form should be reduced to a subspecies of *mazatlanensis*, and Smith and Grant (1958) go a step farther and relegate *nayaritensis* to the synonymy of *mazatlanensis*. The last course seems the most reasonable and is followed here. No obvious differences exist between the specimens from the islands and those from the mainland with which they have been compared.

The *Bufo* secured on the "Puritan" expedition share with *Syrrophus* the distinction of being the first anurans to be found on the Tres Marías Islands. The *Bufo* were obtained from persons who found them about their homes and gardens; none was encountered in the field by members of the expedition, probably owing to the dry conditions prevailing.

Bufo mazatlanensis is peculiar among the reptiles and amphibians of the Tres Marías Islands in that the bulk of its range on the mainland lies to the north of the islands. As presently known, *mazatlanensis* ranges from north-central Sonora to Banderas Bay, Jalisco. Its relationships are with the tropical "*valliceps*" group, otherwise represented in western Mexico only by the little-known *Bufo gemmifer* of Guerrero. Probably *Bufo mazatlanensis* ranges southward from the present known terminus, but it has not yet been found in Colima, which has seen more collecting activity than any other part of the coast between Nayarit and Acapulco.

Syrrhophus modestus pallidus Duellman

Syrrhophus modestus pallidus DUELLMAN, 1958, p. 5, type locality San Blas, Nayarit.

María Magdalena Island (A.M.N.H. Nos. 60392–60398, plus nine untagged); Arroyo Hondo, María Madre Island (A.M.N.H. Nos. 60399–60404, plus 16 untagged).

All frogs were found in the daytime sheltered beneath stones or pieces of wood beside pools or small streams in heavy forest. Search at night on María Magdalena in the same places where the frogs had been taken disclosed no additional individuals, nor were any heard vocalizing. Those from María Magdalena came from an arroyo near the southeastern corner of the island on March 29 and from two branches of an arroyo on the north coast of the island on March 31. The specimens from María Madre Island were collected on April 7. Some of the frogs were found singly, but multiple occurrence was frequent, and on one occasion 13 were under one rock. Descriptions of the places where these frogs were collected are given in an earlier section of this paper.

The following field notes refer to the color and pattern of A.M.N.H. No. 60392 and were made from the freshly killed specimen before preservation: "Dorsal body surface nearly uniform golden brown, excepting some irregular grayish patches. Hind limbs without regular bars, but with irregular darker markings. Forearm with distinct but irregular brownish gray bands. A dark brown face

mask passes from the tip of the snout, bisects the eye, includes the tympanum, and becomes obscure posterior to the forearm insertion. The ventral surfaces are pale and transparent, with a scattering of brown melanophores most numerous in the gular region." Specimen A.M.N.H. No. 60393 was recorded as "The same golden brown [as 60392]. Body surface slightly pustulose, each pustule slightly darker and browner than the background color." These descriptions are at slight variance with the description of the holotype of *pallidus* given by Duellman (1958, p. 6): "In life, the ground color is pale tan and the dorsal markings dark chocolate brown." The differences may merely reflect individual variation in the frogs.

The specimens from the Tres Marías were examined and reported on by Duellman (1958), who assigned them to a new subspecies, *S. modestus pallidus*, found also on the mainland of Nayarit. The typical subspecies, *S. m. modestus*, occurs in Colima and western Jalisco. *Syrrhophus modestus pallidus* shares with *Bufo mazatlanensis* the distinction of being the first amphibian to be reported from the Tres Marías Islands.

Eretmochelys imbricata (Linnaeus)

Testudo imbricata LINNAEUS, 1766, Systema naturae, ed. 12, p. 350, type locality American seas, restricted to the Bermuda Islands by Smith and Taylor, 1950, p. 17.

María Magdalena Island (A.M.N.H. No. 78717).

A member of the crew of the "Puritan" captured this turtle near the bottom in about 20 feet of water at the southeastern edge of the island. The turtle had a carapace length of approximately 17 inches (43 cm.), width of 13 inches (33 cm.), and a weight of 15 pounds. Only the head was saved.

There are no published records for specimens of this species from the territorial waters of Nayarit, but it is well known both north and south of Nayarit.

E. W. Nelson (*in* Stejneger, 1899, p. 64) comments, "The tortoise-shell turtle frequents the sea about the Tres Marías, approaching the shores to mate and deposit eggs in May and June each year."

Chelonia mydas (Linnaeus)

Testudo mydas LINNAEUS, 1758, Systema naturae, ed. 10, p. 197, type locality Ascension Island, South Atlantic.

San Juanito Island (A.M.N.H. No. 78695).

The specimen from San Juanito Island is a skull; remains of several other turtles littered the beach, a testimony to the high esteem in which this species is held by human beings as an article of food.

A large turtle very probably of this species was seen on April 8, approximately 8 miles east-northeast of María Madre Island, where the water at 12.30 P.M. was 23.1° C. (73.5° F.).

According to E. W. Nelson (*in* Stejneger, 1899, p. 64), "the large green sea turtle abounds along these shores [the Tres Marías]."

Kinosternon integrum LeConte

Kinosternum integrum LECONTE, 1854, Proc. Acad. Nat. Sci. Philacelphia, p. 183, type locality Mexico, restricted to Acapulco, Guerrero, by Smith and Taylor, 1950, p. 25.

Cinosternum hirtipes, GÜNTHER, 1885 (1885–1902), p. 15, pls. 12A, 15A–B.

Cinosternum integrum, BOULENGER, 1889, p. 42.

Kinosternon integrum, STEJNEGER, 1899, p. 64. SLEVIN, 1926, p. 202. SMITH AND TAYLOR, 1950, p. 25.

Kinosternon hirtipes, SMITH AND TAYLOR, 1950, p. 25.

Arroyo Hondo, María Madre Island (A.M.N.H. No. 77437).

The only specimen found was captured in the largest of the few small pools in the arroyo (see p. 86). *Kinosternon* has been found only on María Madre Island, to which, in view of the scarcity of water on the other islands, it may be restricted. The species is common on the adjacent mainland and ranges widely from Sonora to Guerrero and eastward to Veracruz.

The two specimens collected by Forrer are identified as *hirtipes* by Günther (1885–1902, p. 15, pls. 12A, 15A–B), but the same specimens are called *integrum* by Boulenger (1889, p. 42). With five specimens collected by Nelson and Goldman available to him, Stejneger (1899, p. 64) had "no hesitation in endorsing Boulenger's view." Smith and Taylor (1950, p. 25) committed themselves

to neither alternative and record both species from the islands. The American Museum specimen was submitted for identification to Dr. Norman Hartweg, who replied (*in litt.*), "This specimen is *K. integrum*, the only species of the genus that gets to the Tres Marías."

In life, A.M.N.H. No. 77437 had the top of the head, carapace, limbs, and tail a nearly uniform, patternless, dull black. The chin and the side of the head were mottled with yellow, and the plastron was yellow, with dark brown markings following the sutures.

On the mainland, *Kinosternon integrum* occurs in small streams or disconnected pools, situations similar to those in Arroyo Hondo. This species probably shares with others of its genus the ability to survive periods of drought, when surface water is unavailable. This ability would be advantageous on the Tres Marías, where the water supply is precarious in the dry season.

Crocodylus acutus Cuvier

Crocodilus acutus CUVIER, 1807, Ann. Mus. Hist. Nat. Paris, vol. 10, p. 55, type locality Santo Domingo.

Crocodylus americanus, STEJNEGER, 1899, p. 64.

Crocodylus acutus acutus, SMITH AND TAYLOR, 1950, p. 211.

The crocodile has been included in the fauna of the Tres Marías on the basis of observations by E. W. Nelson (Stejneger, 1899, p. 64): "The unmistakable furrow in the mud where a crocodile had hauled up on the border of a brackish lagoon on the eastern side of María Magdalena, the sight of a small head in the water, and the testimony of the people on María Madre established the fact of their occurrence. They appeared to be limited to María Magdalena."

Although no specimens are yet known from the Tres Marías, it seems likely that Nelson's sight record will eventually be confirmed by tangible evidence. *Crocodylus acutus* is known from the adjacent coast of Nayarit (Zweifel, 1959c) and is found from Sinaloa and Florida to South America.

Phyllodactylus lanei Smith

Plate 43, figure 2

Phyllodactylus lanei SMITH, 1935, Univ. Kansas Sci. Bull., vol. 22, pp. 125–132, type locality near Tierra Colorada, Guerrero. SMITH AND TAYLOR, 1950, p. 48.

Phyllodactylus tuberculosus, BOULENGER, 1885 (1885–1887, vol. 1), p. 80. GÜNTHER, 1893 (1885–1902), p. 80. STEJNEGER, 1899, pp. 64–65. SLEVIN, 1926, p. 198.

María Madre Island (A.M.N.H. Nos. 78737, 78738, 78763–78766); María Magdalena Island (A.M.N.H. No. 78697).

The specimen from María Magdalena Island was found in a crack in the shale wall of an arroyo; those from María Madre were purchased, so no information on habitat is available. Stejneger (1899, p. 65) and Slevin (1926, p. 198) report specimens taken on houses and under the bark of trees. A notable feature of the pattern of individuals with complete tails is distinct banding distally with black and white, contrasting with the drab grays of the body and proximal part of the tail.

With the addition of María Magdalena Island to the known distribution, the species is now unrecorded only from San Juanito Island. On the mainland, *Phyllodactylus lanei* is said to range from Sinaloa to Guerrero (Smith and Taylor, 1950, p. 48). Other *Phyllodactylus* possibly subspecifically related to *lanei* are found in southern California, Baja California, Sonora, and southward to South America.

Anolis nebulosus (Wiegmann)

Plate 44, figure 1

D[actyloa] nebulosa WIEGMANN, 1834, Herpetologica Mexicana, p. 47, type locality Mexico by inference, restricted to Mazatlán, Sinaloa, by Smith and Taylor, 1950, p. 66.

Anolis nebulosus, GÜNTHER, 1885 (1885–1902), p. 49. BOULENGER, 1885 (1885–1887, vol. 2), p. 77. VAN DENBURGH, 1897, p. 460. STEJNEGER, 1899, p. 65. SLEVIN, 1926, p. 198. SMITH AND TAYLOR, 1950, p. 66.

San Juanito Island (A.M.N.H. No. 77151); María Madre Island (A.M.N.H. Nos. 77144–77150, 77177); María Magdalena Island (A.M.N.H. Nos. 77152–77167); María Cleofas Island (A.M.N.H. Nos. 77168–77176).

The specimens collected on the Puritan-American Museum expedition were sent for examination to Dr. Hobart M. Smith, who reports (*in litt.*) that they are typical *nebulosus* and cannot be differentiated from the

species as it exists on the adjacent mainland. The species is said to range on the mainland from Sinaloa to Oaxaca along the Pacific coast, and inland to Morelos and Puebla, but *A. nebulosus* has been widely confused with *A. nebuloides*, and "virtually all records for both species are . . . open to question" (Smith and Taylor, 1950, p. 66). In any event, the important point is that the insular lizards do not appear to be different from their mainland relatives.

The color of the throat fan is of considerable importance in the classification of *Anolis*. Hence I offer my field notes on a large male individual (snout–vent length 52 mm.) from María Madre Island: "Front margin of throat fan white. The fan is provided with a series of eight rows of white scales. Each row rests upon a yellow stripe, while the yellow stripes alternate with orange stripes which occupy the areas between the rows of white scales." This description is similar to that given by Smith and Grant (1958, p. 19) for a specimen of this species from Puerto Vallarta, Jalisco: "The dewlap in life was deep orange with yellow scale rows and a broad white edge." Referring to specimens from the Tres Marías, Slevin (1926, p. 198) writes, "Males have a large dark red or yellow gular pouch extending along the belly to a point midway between the hind limbs."

Anolis seems to be a lizard of the more heavily forested parts of the islands, where it was always seen in elevated situations on rocks, trees, or logs. There was no indication that the lizards went out of their way to seek the patches of sunlight that filtered down through the forest canopy, and individuals were seen active in the late afternoon after all direct insolation was gone. Body temperatures taken of six active lizards serve to illustrate the relatively low temperatures evidently preferred by the species: 32.4°, 27.5°, 27.2°, 26.0°, 25.2°, and 24.5° C., mean 27.1° C.

A *Dryadophis* collected on María Cleofas had eaten an *Anolis*, as had a *Masticophis* on María Madre.

Ctenosaura pectinata (Wiegmann)

Plate 44, figure 2

Cyclura pectinata WIEGMANN, 1834, Herpetologia Mexicana, p. 42, type locality restricted to Colima, Colima.

Ctenosaura acanthura, BOULENGER, 1885 (1885–1887, vol. 2), p. 196. GÜNTHER, 1890 (1885–1902), p. 57. BAILEY, 1928, p. 16.

Ctenosaura teres, STEJNEGER, 1889, p. 65. SLEVIN, 1926, p. 200.

Ctenosaura brachylopha, BAILEY, 1928, p. 24.

Ctenosaura pectinata, BAILEY, 1928, p. 27. SMITH, 1949, p. 36. SMITH AND TAYLOR, 1950, p. 75.

Ctenosaura parkeri BAILEY, 1928, p. 32.

San Juanito Island (A.M.N.H. No. 78694); María Madre Island (A.M.N.H. Nos. 78651–78656, 78668–78671, 78679–78681); María Magdalena Island (A.M.N.H. Nos. 78790, 78720, 81542).

Spiny-tailed iguanas abound on all four islands. Several purchased on María Madre were trussed up in the customary grisly fashion, with the legs tied over the back by tendons pulled from the toes. The lizards are used as a source of both food and leather by the convicts.

Iguanas are seen on the ground, as well as in more elevated situations such as on stumps, agaves, and in the branches of low trees. An early comment on the habits of these animals in the Tres Marías is that of Grayson (1871, p. 286), who writes: "scarcely a hollow tree in the woods but is occupied by some venerable hermit of this species, who may be seen basking in the balmy air just in front of his door, into which he darts when you approach too near." Some individuals tolerate approach to within an arm's length, but others dash to safety while the intruder is still many yards away. The smaller lizards seemed to be more wary than the old males. The large lizards probably have no enemies other than man and possibly the largest boa constrictors. A *Boa* and a *Drymarchon* collected on the Puritan expedition had each fed upon *Ctenosaura*.

Adult specimens from the islands show considerable variation in color pattern. Some are largely black above, but others have varying amounts of gray, yellow, or reddish brown on the flanks. Young iguanas of this species on the mainland are invariably green; hence it was unexpected to find that insular juveniles had little green in their pattern. The following quotations from my field notes serve as documentation: "Two small individuals, each about 87 mm. snout–vent

length. . . . One has a slight greenish tinge to the wide, brown dorsal cross bands; the narrow interspaces are green. There is some indistinct green mottling on the head. The second specimen shows no sign of green. The body is dark brown with the light interspaces represented by rows of gray spots." These two lizards were brought alive to New York, where they soon assumed the more typical all-over green color, which persisted for months until the lizards died of accident and disease. "[Three] young individuals, snout–vent length about 105 mm. None shows the slightest trace of green. The dorsal body surface has a series of cross bands, about six to eight dark gray-brown ones separated by gray bands one-half to one-third of the width of the darker bands. Tail banded with the same colors."

On the mainland, *Ctenosaura pectinata* ranges from central Sinaloa to Tehuantepec. It also occurs on Isabel Island, between the Tres Marías and the mainland. Two adult iguanas collected on Isabel Island were considerably paler than any encountered on the Tres Marías, but there is so much individual variation in these lizards that the significance of the difference is questionable.

Urosaurus ornatus lateralis (Boulenger)

Plate 43, figure 3

Uta (Phymatolepis) lateralis BOULENGER, 1883, p. 342, type locality Tres Marías Islands and Presidio, Sinaola, restricted to Presidio, Sinaloa, by Oliver, 1943, p. 97.

Uta lateralis, BOULENGER, 1885 (1885–1887, vol. 2), p. 214. GÜNTHER, 1890 (1885–1902), p. 61. STEJNEGER, 1899, pp. 66–67. SCHMIDT, 1921, p. 6. SLEVIN, 1926, p. 198.

Uta ornata lateralis, MITTLEMAN, 1941a, pp. 66–69. OLIVER, 1943, pp. 97–107.

Uta ornata schotti, MITTLEMAN, 1941b, pp. 136–138.

Urosaurus ornatus schotti, MITTLEMAN, 1942, pp. 149–151. SMITH AND TAYLOR, 1950, p. 144.

San Juanito Island (A.M.N.H. Nos. 78688–78693); María Madre Island (A.M.N.H. Nos. 78657, 78658, 78662–78667, 78676–78678, 78740); María Magdalena Island (A.M.N.H. Nos. 78711, 78712).

These lizards are common over the whole of San Juanito Island, which shows little topographic relief and is covered with relatively low, though dense, vegetation. This distribution contrasts with the situation on María Madre and María Magdalena Islands, where the lizards appear to be confined to the beach and low forest immediately behind the beach. It is evident that the heavily forested regions with their reduced light intensity (particularly in the summer rainy season) are unsuited for this lizard. All specimens captured on María Madre Island, and many more seen, were at the edge where grass and herbs impinge upon the sand of the open beach, or were in the scrubby forest (essentially the same vegetation as covers San Juanito Island) behind the beach. On María Magdalena Island a similar situation prevailed. More collecting time was spent inland on this island, but the only *Urosaurus* seen away from the beach was on a rocky ridge on the southwest side of the island. The fact that only two lizards were collected on María Magdalena Island, and 12 on María Madre Island, should not be taken to indicate relative abundance, as no effort was made to gather numerous specimens of the common species. To my remarks on the habitat of *Urosaurus* on the islands may be added those of E. W. Nelson (Stejneger, 1899, p. 66), "this species lives on stones and driftwood near the border of the woods along the sea beaches," and of Slevin (1926, p. 198), "It inhabits the area back of the beach line where it is found among the driftwood and fallen trees."

In view of the ease with which *Urosaurus* can be observed and collected on the three northernmost islands, the lack of specimens from María Cleofas Island indicates that the species is truly absent and not merely overlooked. The habitat appears suitable, but if the species is there, the animals are either excessively rare or were not active at the time of the visit of the "Puritan." Both alternatives seem unlikely. Admittedly, María Cleofas Island has not received so much attention as the other large islands, but I feel that if the lizard occurs there it would have been collected, if not by us, then by Nelson or by W. H. Burt, who collected *Urosaurus* on María Magdalena and other lizards (but not *Urosaurus*) on María Cleofas (specimens in the collection of the Museum of Zoölogy, University of Michigan).

In addition to the peculiarity of distribution within the Tres Marías Islands, there is the unique situation that *Urosaurus* is the only species of reptile or amphibian known from the islands that is widely distributed on the mainland to the north, but apparently does not range so far south on the mainland as the latitude of the islands. These oddities of distribution are discussed more fully below in this paper. The subspecies *lateralis* ranges from southern Sonora southward an undetermined distance into Sinaloa, possibly but not certainly as far as Presidio near Mazatlán. Elsewhere the species ranges widely over the southwestern United States and northern Mexico (fig. 5).

Cnemidophorus communis mariarum Günther

Cnemidophorus mariarum GÜNTHER, 1885 (1885–1902), p. 28, type locality Tres Marías Islands.

Cnemidophorus sexlineatus mariarum, MERTENS, 1934, p. 36.

Cnemidophorus communis mariarum, ZWEIFEL, 1959a, p. 79.

San Juanito Island (A.M.N.H. Nos. 78684–78687); María Madre Island (A.M.N.H. Nos. 78659–78661, 78739, 78762); María Magdalena Island (A.M.N.H. Nos. 78698–78708, 78713–78715, 79046); María Cleofas Island (A.M.N.H. Nos. 78726, 78729).

This species was discussed in a recent publication (Zweifel, 1959a) to which the reader is referred for a more detailed synonymy and discussion of variation and relationships. Briefly, the insular populations constitute a well-differentiated endemic subspecies of a species that ranges on the mainland from coastal Jalisco to Michoacán and perhaps to Central America.

At the time of the visit of the "Puritan," only juvenile individuals of *Cnemidophorus* were active, although a single adult was found beneath a rock. No habitat restriction was evident, but lizards were most abundant where a break in the forest canopy, such as follows an arroyo, permitted sunlight to reach the ground unfiltered. Many more lizards were seen on the three northern islands than were collected, but the two individuals from María Cleofas were the only whiptails seen there. It may be that the condition of relatively undisturbed forest on María Cleofas, together with the absence of large arroyos breaking the canopy, renders the habitat less suitable for a strictly ground-dwelling animal with the high temperature requirements of *Cnemidophorus*. During the summer rainy season, when adult lizards are most active, the leafing out of the forest would probably render the habitat even less suitable. Nelson and Goldman (Stejneger, 1899, p. 68) collected five *Cnemidophorus* on a barren, outlying rock off María Cleofas, but obtained only a single specimen on the island.

Boa constrictor imperator Daudin

Plate 44, figure 3

Boa imperator DAUDIN, 1803, Historie naturelle . . . des reptiles, vol. 5, pp. 150–152, type locality Mexico. STEJNEGER, 1899, p. 69. SLEVIN, 1926, p. 202.

Constrictor constrictor sigma, SMITH, 1943, pp. 411–412. SMITH AND TAYLOR, 1945, p. 25.

Constrictor constrictor imperator, SMITH AND TAYLOR, 1945, p. 25.

Boa constrictor sigma, FORCART, 1951, p. 199.

María Madre Island (A.M.N.H. Nos. 78672, 78673, 78736); María Magdalena Island (A.M.N.H. Nos. 78710, 78723); María Cleofas Island (A.M.N.H. Nos. 78730, 78732 [skull only]).

Smith and Taylor (1945, p. 25) record this species only from María Madre Island, though Slevin (1926, p. 202) mentions that the species was collected on María Magdalena. The collections of the Puritan-American Museum expedition add another island, María Cleofas, to the known range.

The snakes from María Madre Island, including one still alive at the present writing and hence not in the list of specimens, were obtained by purchase. An adult found on María Magdalena Island on March 29 was taken in the arroyo described on page 87. The snake was submerged in a small pool almost completely filled with leaves and was not observed until leaves were scraped away, uncovering it. Another adult specimen from María Magdalena taken on the evening of March 31 was found under very similar conditions, buried in moist leaves at the foot of a cliff in a canyon described on pages 87–88. Both these snakes were relatively free of external parasites, in striking contrast to one from María Cleofas found coiled at the root

buttress of a fig tree under very dry conditions. This snake was infested with countless ticks (*Amblyomma dissimile* Koch), some almost a centimeter in length. Possibly the snakes are able to discourage such heavy infestations by prolonged submergence where water is available. The digestive tract of one *Boa* was crammed with plant material, evidently from a *Ctenosaura* the snake had eaten.

A.M.N.H. No. 78723 possibly represents a record length for the Mexican boa constrictor. Freshly killed, this female measured 7 feet 6 inches (2285 mm.) in total length, of which 9 inches (229 mm.) was tail. The weight, as determined independently on two relatively crude, sportsman's, fish-weighing scales, was 13 pounds. The snake was preserved as an alcoholic skin, with head and tail intact. Though no effort was made to stretch the skin, it measures 8 feet 8 inches. With reference to the size of the boa in Mexico, Smith (1943, p. 411) writes: "I have never seen a specimen in the field that would exceed perhaps 7 feet in total length, and the largest measured specimen is a dried, stretched skin of about 2,420 mm. in total length (7.9 feet)." A boa in the possession of convicts on María Madre appeared to be at least as large as the specimen from María Magdalena, but we were unable to secure the snake or make a precise measurement. Bogert and Oliver (1945, p. 350) repeat an oral report that these snakes reach a length of 9 feet in southern Sonora, Mexico, and I suspect that the specimen from María Magdalena Island does not represent the maximum size for the subspecies.

The boa of the Tres Marías Islands was named an endemic subspecies, *Constrictor constrictor sigma*, by Smith (1943, pp. 411–412). The only diagnostic character given is the greater number of ventral scales in the insular population, 258–259 in three specimens, as opposed to 225–253 (mean 241.6) in 61 specimens from the mainland. When the counts for specimens in the American Museum are combined with published records, the range in the population of the Tres Marías is 253–260 scales, mean 257.0, based on nine specimens. The sample includes both male and female snakes, as sexual dimorphism appears to be insignificant or absent. Although there is a slight overlap in ranges of variation, the island snakes remain obviously different. However, the taxonomic (not statistical) significance of such differentiation is open to question, and in accord with the policy adopted here in the treatment of insular populations, I consider it best to relegate *sigma* to the synonymy of *imperator*.

The boa constrictor is a widely distributed species, ranging from Sonora and Tamaulipas southward well into South America. The range of the subspecies *imperator* includes all of the area mentioned above as far as northern South America.

Dryadophis melanolomus slevini (Stuart)

Eudryas slevini STUART, 1933, p. 9, type locality María Madre Island, Tres Marías Islands.

Drymobius boddaertii, GÜNTHER, 1894 (1885–1902), p. 126. BOULENGER, 1894 (1893–1896, vol. 2), pp. 12–13. STEJNEGER, 1889, p. 69. SLEVIN, 1926, p. 201 (part).

Dryadophis melanolomus slevini, STUART, 1941, pp. 93–95. SMITH, 1943, p. 418. SMITH AND TAYLOR, 1945, p. 52.

María Magdalena Island (A.M.N.H. Nos. 76215, 78718, 78719); María Cleofas Island (A.M.N.H. No. 78728).

One of the snakes from María Magdalena is a juvenile collected by Kenneth Stager on April 24, 1955. The other two specimens from that island, an adult and a juvenile, were found in the daytime on March 31 near water in cool, shady arroyos. The single specimen from María Cleofas represents the first record of the species for that island. It was captured on April 3, in dry, tall forest and had eaten an *Anolis*. Snakes of this species were parasitized by the tick *Amblyomma dissimile* Koch.

The *Dryadophis* of the Tres Marías was named an endemic species by Stuart (1933). At that time he had no specimens of the genus from the mainland of western Mexico north of the Isthmus of Tehuatepec. In a review of the genus *Dryadophis*, Stuart (1941) referred insular and mainland populations of western Mexico to a single species and subspecies, but noted that there was considerable variation in the small sample available to him and that as many as three distinct races may be involved in the region from Guatemala to Colima and the Tres Marías. With

several additional specimens on hand, Smith (1943, pp. 418–421) redefined the insular population as an endemic subspecies and described additional races from the mainland. The principal differences between *D. melanolomus stuarti* of the mainland and *D. m. slevini* of the islands are in pigmentation of adult individuals. The single adult specimen in the American Museum of Natural History agrees with the characters of *slevini* as given by Smith.

In addition to the differences in color pattern between *slevini* and *stuarti*, Smith (1943, p. 420) mentioned a difference in average number of ventral scales that seems to add weight to the argument favoring subspecific distinction for the insular population. There are, however, several factors to be taken into consideration before the situation with regard to ventral scutellation can properly be assessed. First of all, Smith unfortunately accepted six counts published by Slevin (1926, p. 201). In reading Slevin's paper, I was struck by his statement that *Drymobius boddaertii* (=*Dryadophis melanolomus slevini*) was the commonest snake collected on the islands. In my experience, this distinction belonged to *Masticophis lineatus*, a species that Slevin did not record. The suspicion that Slevin may have misidentified the snakes was verified by the receipt of a list of Tres Marías specimens in the collection of the California Academy of Sciences. In this list, kindly furnished by Dr. Alan Leviton, only a single specimen of "*Drymobius*" (C.A.S. No. 58679) is recorded, but there are five "*Coluber lineatum*" (C.A.S. Nos. 58676–58678, 58990, 58991). Evidently the correction of identification was made many years ago, for when Stuart (1933) described *Eudryas slevini*, C.A.S. No. 58679 was named type specimen and no others in that collection were mentioned. Unfortunately, no notice of the reidentification was published, and Smith was led to believe that *Dryadophis* on the islands showed a wider range of variation in number of ventral scales than is actually the case.

Another factor that must be taken into consideration is sexual dimorphism. The data presented by Smith (1943) in his descriptions of new subspecies of *Dryadophis* indicate that dimorphism is present, though the matter is not discussed. Counts in the literature together with those of specimens in the American Museum may be summarized as follows[1]: *D. m. slevini*, males (four specimens), mean 184.2, range 182–187; females (four specimens), mean 188.7, range 186–190; *D. m. stuarti*, males (10 specimens) 179–185, mean 179.8; females (11 specimens) 180–190, mean 185.1. Sexual dimorphism in the two subspecies is similar, to judge from the small samples available. There appears to be a slightly greater number of ventral scales on the average in the insular population, although the difference is less than Smith (1943, p. 420) was led to believe by the erroneous data available to him.

Unlike the several populations of insular snakes that are differentiated only in number of ventral scales, *Dryadophis* exhibits in addition characters of color pattern that will, according to Smith, distinguish insular and mainland populations at a glance. In view of this increased degree of differentiation, recognition of the snakes of the Tres Marías Islands as comprising an endemic subspecies seems warranted.

The *Dryadophis* of the Tres Marías Islands lie at a more northerly latitude than the northernmost known population of the mainland. A recent record of *Dryadophis m. stuarti* at Banderas Bay, Jalisco (Smith and Grant, 1958, p. 22), extends the range northward on the mainland to within 80 miles of María Cleofas Island, and it seems likely that the species occurs in southern Nayarit. Elsewhere, *D. melanolomus* in various subspecific forms ranges southward on both coasts to Panama.

Drymarchon corais rubidus Smith

Drymarchon corais rubidus SMITH, 1941b, pp. 474–476, type locality Rosario, Sinaloa.

Spilotes corais, GÜNTHER, 1894 (1885–1902), p. 116.

Coluber corais, BOULENGER, 1894 (1893–1896, vol. 2), p. 32.

Drymarchon corais melanurus, STEJNEGER, 1899, p. 70. SLEVIN, 1926, p. 202.

Drymarchon corais cleofae BROCK, 1942, pp. 249–250, type locality María Cleofas Islands, Tres Marías Islands. SMITH, 1943, p. 421. SMITH AND TAYLOR, 1945, p. 54.

[1] Dr. Hobart M. Smith kindly furnished information on the sex of certain specimens for which scale counts have been published.

María Madre Island (A.M.N.H. No. 78760); María Magdalena Island (A.M.N.H. Nos. 78722, 78724); María Cleofas Island (A.M.N.H. No. 78727).

A small individual from María Magdalena was found at the edge of a canyon pool, but a large adult from that island and another from María Cleofas were in the forest far from any water. All were found during daylight hours. One adult had eaten a *Ctenosaura*, and another consumed a small *Dryadophis* when the two were confined in the same collecting sack. Specimens of the tick *Amblyomma dissimile* were taken from *Drymarchon*.

Two adult specimens, each approximately 6 feet in length, showed slight differences in ventral color. The chin and light areas of the ventrals in the specimen from María Magdalena were white. The same colors are present in the specimen from María Cleofas, but the ends of the ventrals on the anterior one-third of the body were reddish brown in life. The colors of an adult specimen from María Magdalena were recorded by Slevin (1926, p. 202) as "anterior gastrosteges white, spotted or edged with black; gular region white." According to Smith (1941b), the belly scales of *rubidus* are salmon pink. However, his observations may be based on individuals from the southern part of the range, and the apparent difference between insular and mainland populations may not be real. My own recollection, unfortunately not verified by on-the-spot notes, of *Drymarchon* in southern Sonora is that little red is present.

The indigo snake of the Tres Marías Islands was segregated as an endemic subspecies, *D. c. cleofae*, by Brock (1942) on the basis that more ventral scales are present than are seen in specimens from the mainland of western Mexico. Brock presents data on his single specimen and counts published by Boulenger (1894 [1893–1896, vol. 2]) and Smith (1941b) for three other individuals. Evidently he overlooked the published data of Slevin (1926) referring to a fifth specimen. To the ventral counts of these five specimens may be added those of the four in the American Museum. The average of these nine counts is 203.0, range 200–209. It should be mentioned that sexual dimorphism, if present, is too slight to be of concern. Data are available for 27 specimens from the mainland of western Mexico (counts published by Smith, 1941b, and Bogert and Oliver, 1945). The mean of these counts is 194.7, range 190–201. It is evident that the difference in means detected by Brock is supported by the additional data now available. The matter in question is the advisability of bestowing taxonomic recognition on a population that is distinguishable evidently only by a slight (even though statistically significant) difference in average number of ventral scales. I have adopted the viewpoint of Bogert and Oliver (1945, pp. 360–361) that insular races based solely on differences in ventral and subcaudal counts are not worthy of taxonomic recognition. Hence I refer the snakes of the Tres Marías Islands to the race of the adjacent mainland, *D. c. rubidus*. The race *rubidus* ranges from southern Sonora to Tehuantepec, and the distributional area of the species as a whole takes in subtropical and tropical regions from Florida to South America.

Exelencophis nelsoni (Slevin)

Tantilla nelsoni SLEVIN, 1926, p. 200, type locality María Madre Island, Tres Marías Islands. MERTENS, 1934, p. 36.

Exelencophis nelsoni, SMITH, 1942a, p. 33. SMITH AND TAYLOR, 1945, p. 62.

The identity and relationships of this "lost" species present one of the more intriguing problems in the herpetology of Mexico. The original description by Slevin (1926, pp. 200–201) is disappointingly brief. As a basis for discussion, the description is quoted below:

"*Diagnosis.*—Rostral small, a little broader than deep, scarcely visible from above; frontal large, a little longer than broad; nostril in a single nasal; symphyseal in contact with anterior genials; anterior genials twice as long as posterior. Scales smooth, in 15 rows, gastrosteges 130, urosteges 39c, anal single, supralabials 7-6, infralabials 8-8, preoculars 1-1, postoculars 2-2, temporals 1+2-1+2. Color black, with eleven complete white bands four to five scales wide encircling the body; three encircling the tail; tip of tail white; a narrow white band crosses the back of the head touching the posterior tips of the parietals; snout and top of head, uniform black; anterior labials black, edged with

white; posterior labials white; throat white.

"*Type:* No. 58680, Mus. Calif. Acad. Sci., María Madre Island, Tres Marías Islands, Mexico, collected by a native, May 18, 1925.

"Named for Lieutenant M. M. Nelson, U. S. Navy, commanding officer of the U.S.S. *Ortolan.*"

When Smith (1942a) reviewed the Mexican snakes of the genus *Tantilla*, he erected a new genus, *Exelencophis*, for the species *Tantilla nelsoni*. The basis for the new genus is that not only are the characters given by Slevin for the species not those of the genus *Tantilla*, but the combination of characters is unique among all snakes. Unfortunately, any check upon Slevin's description is impossible, as the type and unique specimen was lost in the mails sometime previous to Smith's work on the genus *Tantilla*.

One of the notable features of the herpetofauna of the Tres Marías is that there is relatively little differentiation from mainland parental stocks. Except for *E. nelsoni*, there are no endemic species, and though several endemic subspecies have been recognized, all are clearly related to (and in some cases virtually identical to) populations on the mainland. In this context the presence of an endemic species, much more an endemic genus, is open to question.

In view of the distribution on the mainland of the species comprising the Tres Marías herpetofauna, it seems reasonable to search for the relatives of *Exelencophis* among the species of snakes inhabiting the region from southern Sinaloa to Guerrero. Within this region, approximately 90 species of snakes (some with several subspecies) have been found. With this abundance of forms to choose from, it would seem that a close relative of *Exelencophis* might be found. Such, however, is not the case. The majority of species can be eliminated from consideration as vastly different in scutellation and color pattern from *Exelencophis*. There are 14 species with color pattern more or less resembling that of *Exelencophis* in that the pattern consists of dark and light rings, or broad transverse blotches that might conceivably be modified into rings. Most of these can be eliminated from consideration on the basis of several characters not shared with *Exelencophis*. In the following paragraphs I mention only a few of the more obvious characters.

Dipsas gaigeae: Scale rows (13) are similar to those of *Exelencophis* (15), but ventrals and subcaudals (168, 70) are much too numerous. It is unlikely that Slevin would have referred his species to the genus *Tantilla*, with which he was familiar in western North America, if it possessed the peculiar habitus of *Dipsas*.

Lampropeltis triangulum: The presence of this species on the Tres Marías Islands makes it unlikely that *Exelencophis* is a relative. This view is substantiated by considerable differences in morphology and color.

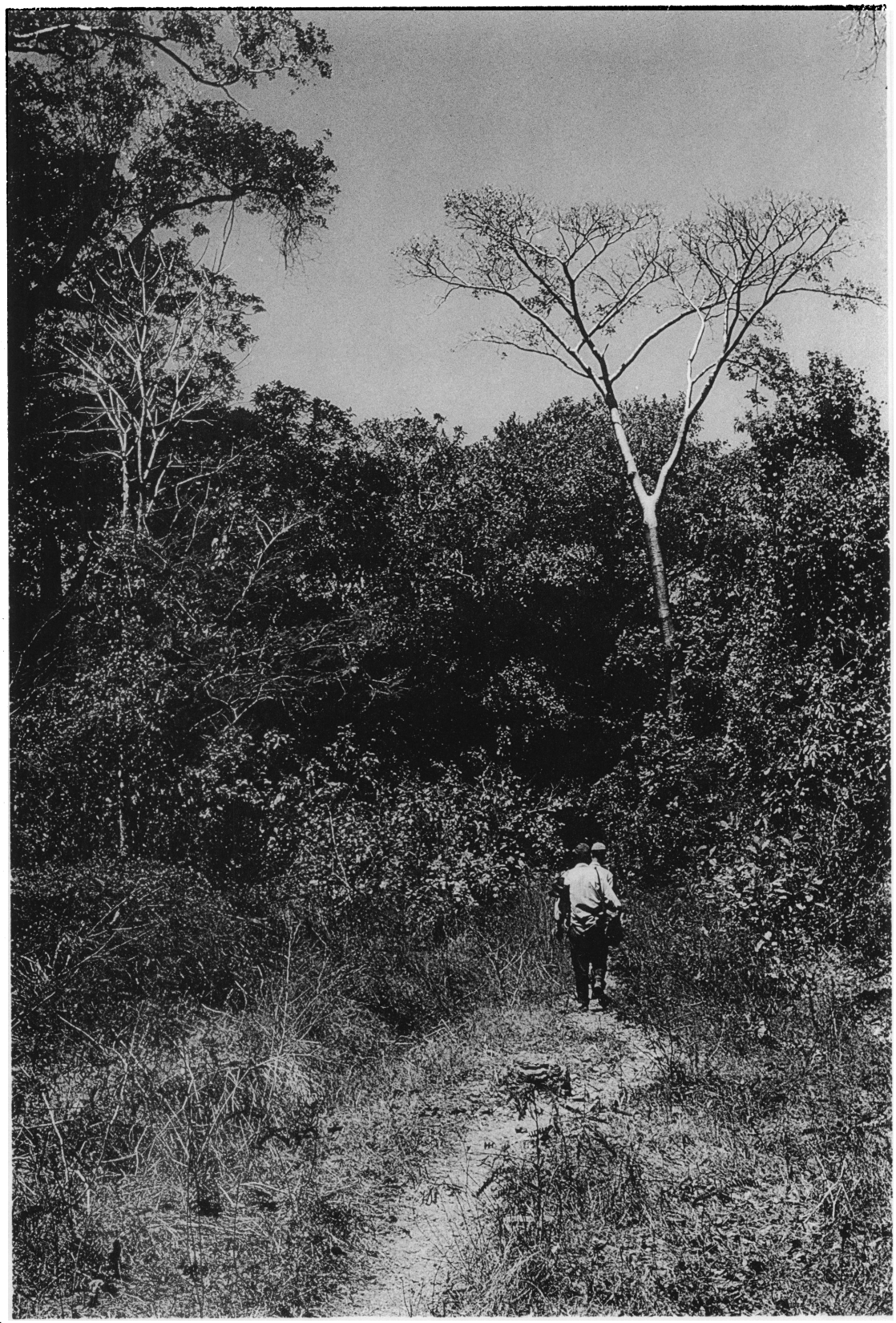
Rhinocheilus lecontei: Some individuals of *Rhinocheilus* have very little red in the pattern and thus resemble *Exelencophis*. However, scale rows (23 at midbody) and ventrals (193–204) are much more numerous, and several additional details of scutellation differ as well.

Sympholis lippiens: The black and white ringed pattern of this species is quite similar to that of *Exelencophis*, but again characters of scutellation belie any close relationship. Ventral scales number over 200 in *Sympholis*, subcaudals are fewer (23 and 24 in two specimens), and scale rows more numerous (19 at midbody).

Tropidodipsas: Three species of this genus are found in the area in question: *T. philippi*, *T. occidentalis*, and *T. fasciata guerreroensis*. Only one of these, *occidentalis*, has rings that cross the belly. Ventral scales are more numerous in all species (175 or more), and subcaudals much more numerous (81 in the type specimen of *occidentalis*).

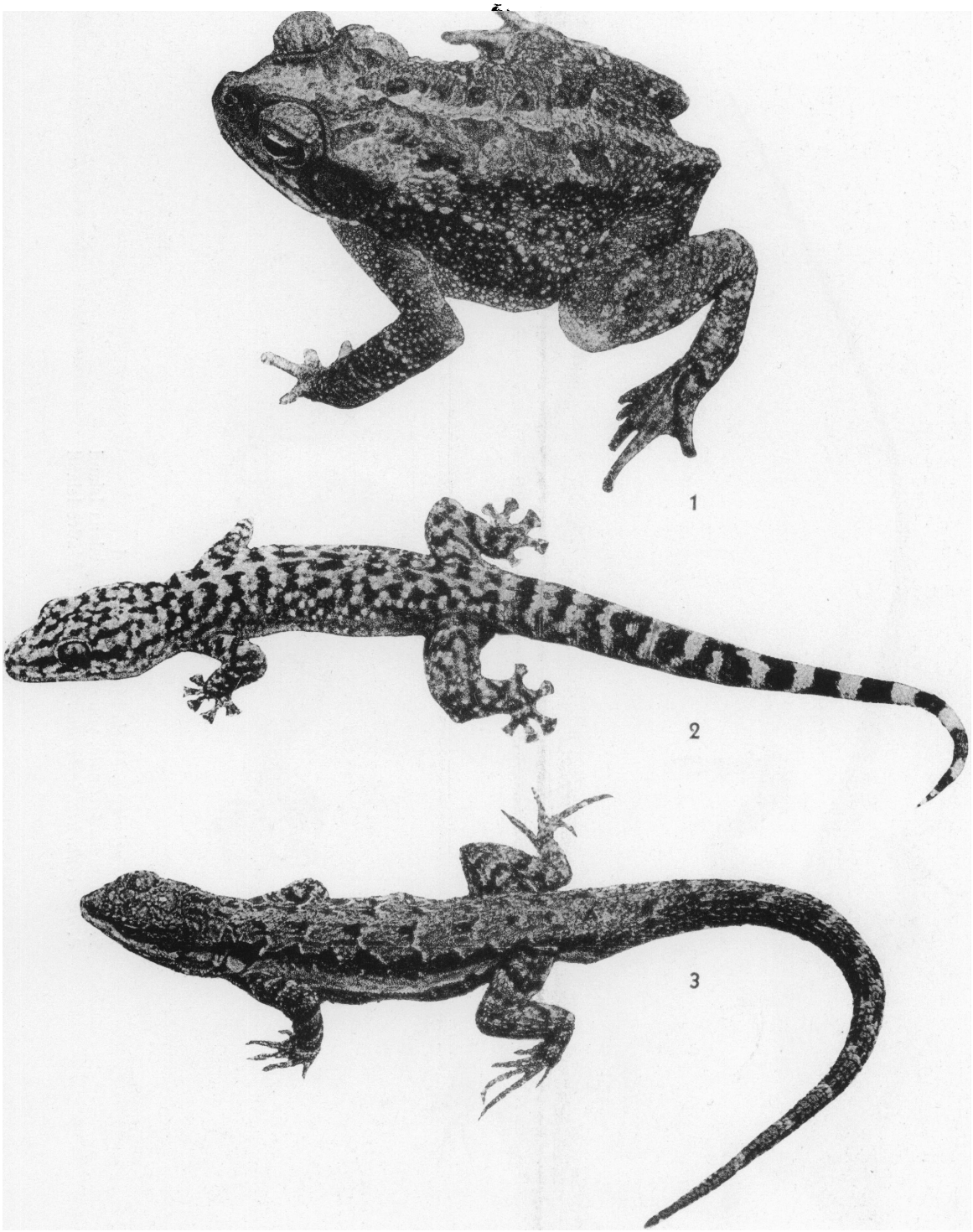
Micrurus and *Micruroides:* Six species of coral snakes are *Micruroides euryxanthus*, *Micrurus diastema*, *M. distans*, *M. laticollaris*, *M. nigrocinctus*, and *M. nuchalis*. All have ventral scales much more numerous (190 or more) than does *Exelencophis*, and all show considerable red in the pattern.

Geatractus tecpanecus: This species is known from only a single specimen which is in very poor condition (Smith and Necker, 1943). Scale rows are 15, as in *Exelencophis*, but the scales are faintly keeled posteriorly, not

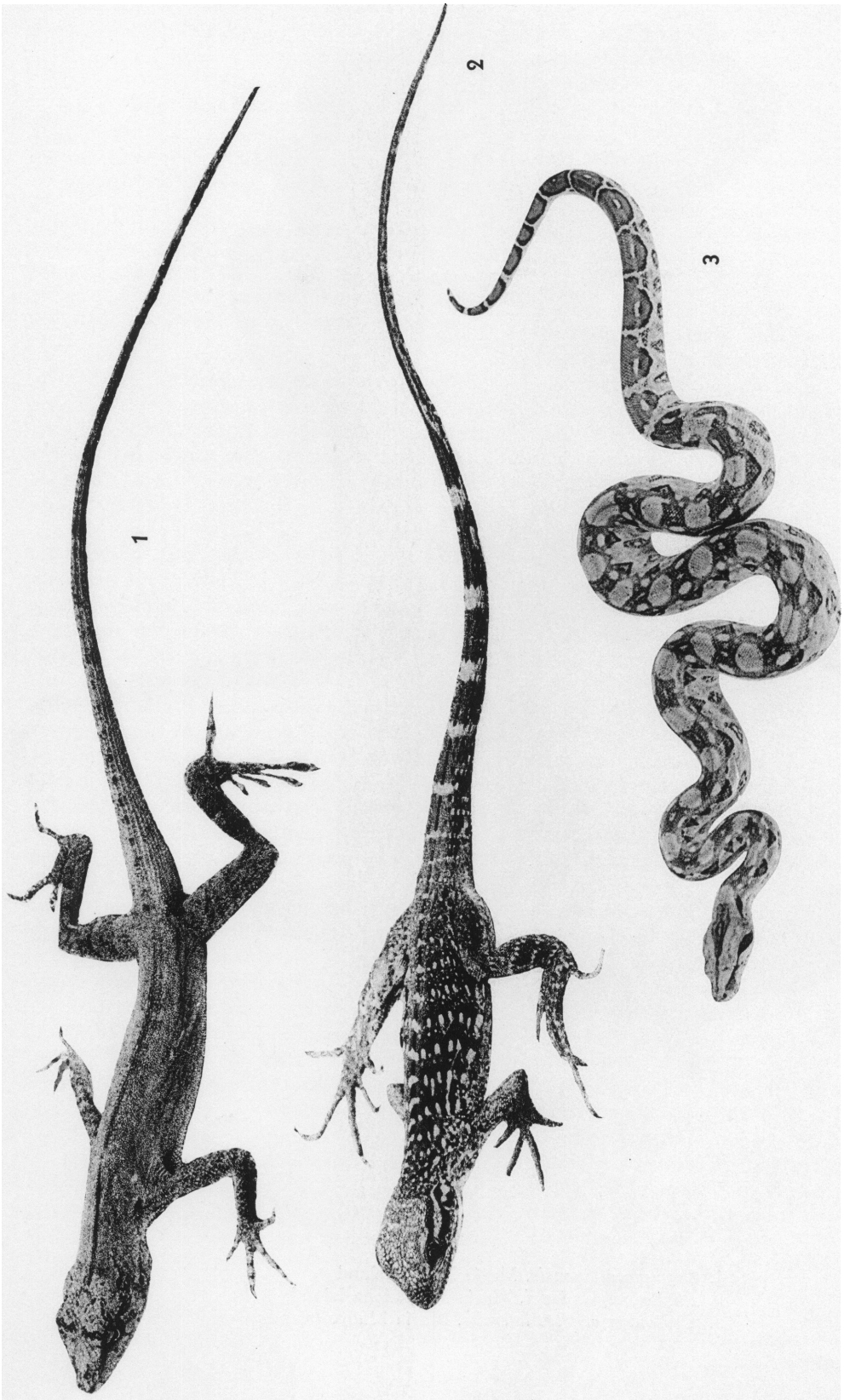


Scene in Arroyo Hondo, María Madre Island, taken from a clearing in the forest

Scene on San Juanito Island, showing a road through the dense Thorn Forest



1. *Bufo mazatlanensis*, María Madre Island
2. *Phyllodactylus lanei*, María Magdalena Island
3. *Urosaurus ornatus lateralis*, María Madre Island



1. *Anolis nebulosus*, María Magdalena Island
2. *Ctenosaura pectinata*, young, María Magdalena Island
3. *Boa constrictor imperator*, young, María Madre Island

smooth. Other points of similarity in scutellation are the single anal scute, a large loreal entering the orbit (perhaps equivalent to the "preocular" in *Exelencophis*), the number of ventral scutes (estimated as at least 136), six supralabials (six on one side only in *Exelencophis*), and two postoculars on one side (two on both sides of *Exelencophis*). Points of dissimilarity are the presence of a divided nasal and the separation of the mental shield from the anterior chin shields by the first infralabials which meet medially. The pattern of *Geatractus* consists of light dorsal bands one to one and one-half scales in width, rather than light rings four to five scales in width. The ringed pattern might well be derived from the pattern of *Geatractus*.

Chersodromus annulatus: Like *Geatractus*, which it resembles, this species is known from only a single specimen (Zweifel, 1954). In several respects *C. annulatus* is more like *Exelencophis* than any other species of the adjacent mainland. The color pattern is closely similar, the ventrals and subcaudals (140, 41) are of similar number, the anal plate is single in both, the supralabials number six in *annulatus* and six on one side of *Exelencophis*, the single preocular in *Exelencophis* is possibly equivalent to the loreal (=preocular) in *annulatus*, the temporals are one plus two in both species, and the anterior chin shields are twice the length of the posterior ones in both. Points of dissimilarity are these: prefrontals of *C. annulatus* fused into a single scale, presumably normal in *Exelencophis* (may be abnormal in *C. annulatus*); scale rows 17 instead of 15, and all but three lower rows keeled, not smooth; anterior chin shields separated from mental by infralabials rather than in contact as in *Exelencophis;* nostril on the suture between two nasals rather than pierced in a single nasal.

On the basis of information available at the present time, it is not possible to relate *Exelencophis nelsoni* to any species known to occur on the mainland of western Mexico. If one were to assume that some of the characters given in the description of *nelsoni* were incorrect as a result of errors in determination or printing, new avenues of study would be opened up. However, I prefer not to compound the confusion by attempting to refute what little we apparently know about this elusive species.

Imantodes gemmistratus latistratus (Cope)

Dipsas gemmistrata latistrata COPE, 1887, Bull. U. S. Natl. Mus., no. 32, p. 68, type locality "Guadalajara," Jalisco, Mexico (probably in error, Zweifel, 1959b).

Himantodes gracillimus, BOULENGER, 1896 (1893–1896, vol. 3), p. 87 (part).

Imantodes gracillimus, SMITH, 1942c, p. 387 (part). SMITH AND TAYLOR, 1945, p. 76 (part).

Imantodes gemmistratus latistratus, ZWEIFEL, 1959d, p. 3.

This species is known from the Tres Marías only from a single specimen taken by Forrer, presumably on María Madre. The taxonomy and distribution of *Imantodes* in western Mexico have recently been reviewed (Zweifel, 1959d), so little additional comment is required here.

The specimen from the Tres Marías has 253+ ventral scales, a number that is several more than the maximum of 236 noted among specimens of *latistratus* from the mainland and equals the maximum of the subspecies *gracillimus*. So far as can be determined from the published description (Boulenger, 1896 [1893–1896, vol. 3], p. 87), the color pattern of the Tres Marías specimen is that of *latistratus* rather than *gracillimus*. The increased ventral count over that seen in mainland *latistratus* may be merely another example of a phenomenon common to many insular serpents. From the standpoint of present-day geography, either *latistratus* or *gracillimus* (or an intermediate population) could be ancestral, as the two forms intergrade at Banderas Bay in northwestern Jalisco, in the region where the connection between the islands and mainland may have existed at one time. The range of *Imantodes gemmistratus* is from southern Sonora and central Veracruz to Panama.

Lampropeltis triangulum schmidti Stuart

Lampropeltis triangulum schmidti STUART, 1935, p. 2, type locality Tres Marías Islands (exact island unknown, but probably María Madre). SMITH, 1942b, p. 200. SMITH, 1943, p. 438. SMITH AND TAYLOR, 1945, p. 84.

Coronella micropholis, BOULENGER, 1894 (1893–1896, vol. 2), p. 204.

Coronella annulata, GÜNTHER, 1894 (1885–1902), p. 109.

Lampropeltis micropholis oligozona, STEJNEGER, 1899, p. 70.

Lampropeltis triangulum nelsoni, BLANCHARD, 1920, p. 6 (part); 1921, p. 157 (part).

Lampropeltis doliata schmidti, KLAUBER, 1948, p. 11.

María Madre Island (A.M.N.H. Nos. 78674, 78761).

The specimens obtained on the Puritan expedition were purchased, so no exact habitat data are available.

The king snake of the Tres Marías Islands was given the subspecific name *schmidti* by Stuart (1935), who examined the only four specimens then in collections and found them distinct in pattern and scutellation from snakes of the mainland.

A brief survey of variation is necessary before inferences as to the relationships and systematic status of the insular snakes can be presented. Adequate comparison of insular and mainland populations is difficult, because *Lampropeltis triangulum* in western Mexico is poorly known.

Pattern characters of importance in the subspecific classification of western *Lampropeltis triangulum* are these: (1) snout color (jet black to a pale extreme in which the rostral, nasals, internasals, loreals, prefrontals, and anterior supralabials are largely or wholly pale); (2) width of pale ring on head (posterior margin of ring on last supralabial to two scales behind angle of mouth); (3) number of pale annuli on body (10 to 25, excluding the head ring); (4) width of pale rings (one to three and one-half scales in width along the midline); (5) pale rings immaculate or spotted with gray; (6) width of black rings (rings may meet on midline at expense of red rings or may be considerably narrower than adjacent red rings); (7) presence or absence of black spotting in red rings.

Some of these characters obviously are correlated. Thus snakes with very broad red rings have the total number of rings reduced, and the width of yellow and black rings narrowed as well. Ontogenetic variation may be present in the spotting of pale rings with gray, with the spotting most prominent in larger snakes.

The king snakes of the coastal region of western Mexico are at present assigned to three subspecies: *nelsoni*, ranging from southern Sonora to Colima and inland to Guanajuato; *schmidti* on the Tres Marías Islands, with a single mainland record on the coast of Jalisco; and *blanchardi* of Guerrero. Another form, *arcifera*, enters the picture from the east on the Plateau.

Although Smith (1942b) emphasized that *L. t. nelsoni* is a highland subspecies, specimens from the foothills and coastal plain as far north as southern Sonora were referred to *nelsoni* by subsequent authors (Bogert and Oliver, 1945; Zweifel and Norris, 1955; Smith and Van Gelder, 1955; Tanner and Loomis, 1957). Snakes from the coastal plain of Nayarit (including Isabel Island) northward to Sonora are distinct from *nelsoni* of the Plateau and probably deserve separate taxonomic status. The principal distinguishing character of the north coastal population is great expansion of red areas, with consequent reduction in number of annuli and width of black and white rings. The immaculate white rings number 10 to 13 on the body in nine specimens, and are one to one and one-half scales in width middorsally. The scales of the red wings are immaculate, without black tips. In life the snout is mottled with white. The white ring on the head is narrow. Two specimens from Sonora, four from Sinaloa, and two from Isabel Island have the posterior margin of the ring on the last supralabial or at most one-half of a scale behind the angle of the mouth. A snake from Acaponeta, Nayarit, though resembling other north coastal specimens in body pattern, has a broader ring, with the rear edge one and one-half scales back. Reduction of black and white is carried to an extreme in one specimen from Isabel Island (S.D.S.N.H. No. 17571). The middorsal region from nape to base of tail is red; there are no complete white or black annuli on the body, the 13 presumptive annuli all being interrupted dorsally. However, complete triads are present on the tail. Another specimen from Isabel Island (U.M.M.Z. No. 84256) has the normal ringed pattern, so the peculiar specimen may merely be a variant individual and not characteristic of a differ-

entiated insular population. Examples of the north coastal form are illustrated by Bogert and Oliver (1945, fig. 4 and pl. 32).

The type locality of *Lampropeltis triangulum nelsoni* (Blanchard, 1920, p. 6) is Acambaro, Guanajuato. I have examined the type specimen (U.S.N.M. No. 46552) as well as one other from Guanajuato (U.S.N.M. No. 12680), four specimens in the collection of the American Museum from the vicinity of Magdalena and Hostotipaquillo in western Jalisco and one from San Juan Peyotán, Nayarit, that I regard as representing *nelsoni* in the restricted sense. These snakes (except the specimen from Nayarit, which lacks the head) are similar to coastal "*nelsoni*" in snout pattern, but differ in number of pale body rings (14 to 17, as against 10 to 13). The pale ring on the head is broader in specimens of *nelsoni* from Jalisco and Guanajuato, all of which have the posterior edge of the ring behind the angle of the mouth, one to one and one-half scales back in most instances. The pale rings on the body are one and one-half to two and one-half scales in width, compared to one to one and one-half scales in the coastal specimens. These body rings are flecked with gray in some large specimens of both coastal and inland specimens, but the red rings are immaculate in both.

The relationship of what I consider typical *nelsoni* to populations other than north-coastal "*nelsoni*" is as yet not clear, mainly because of inadequate material. Two specimens from Colima (U.S.N.M. Nos. 31492 and 31493) resemble *nelsoni* in having 14 and 15 light rings on the body speckled with gray, a broad head ring extending two scales behind the angle of the mouth, and immaculate red rings. The snout, however, is much lighter than seen in any *nelsoni*, with all scales from rostral to prefrontals inclusive being almost totally pale. The pale body rings are two to two and one-half scales in width, perhaps slightly wider than is usual in *nelsoni*. The light snout and wide body rings are characters suggestive of *L. t. schmidti*.

A specimen from the west end of Lake Chapala, near Jocotepec, Jalisco (A.M.N.H. No. 71364), deviates from *nelsoni* in these ways: the snout is black rather than mottled; the head ring is narrow, the posterior margin being on the last supralabial; there are 20 pale body rings, more than are seen in *nelsoni;* and the scales of the red areas are darker at the tip than is true in *nelsoni*, though the tips are not black. The black snout, narrow head ring, and dark scale tips relate this specimen to *L. t. blanchardi* of Guerrero.

A specimen from Jamay, on the northeastern shore of Lake Chapala (A.M.N.H. No. 19650), also differs in some respects from *nelsoni*. The snout is dark, and the head ring narrow, with the posterior margin at the angle of the mouth. There are 16 pale rings one to two scales in width on the body, which is characteristic of *nelsoni*, but the black rings are as wide as or wider than the red rings dorsally, and in one instance two black rings are confluent. The red rings are unspotted. The narrow head ring and expansion of black body rings may represent tendencies towards *L. t. arcifera*, which is known from 15 kilometers west of Morelia, Michoacán, about 100 miles east-southeast of Jamay, and which has "black rings very broad, encrouching dorsally" (Smith, 1942b, p. 198).

Peters (1954, p. 24) reports two specimens from Coalcomán, Michoacán, that have the mottled snout of *nelsoni* combined with black-tipped scales in the red rings characteristic of *blanchardi*, and "suggests the possibility that they are intergrades" between *nelsoni* and *blanchardi*. His specimens have unusually high numbers of pale rings on the body, 22 and 25. Data are available on five specimens of *blanchardi* from Guerrero, which have 14 (twice) or 15 (three times) body rings. I have examined only a single specimen from Michoacán (U.S.N.M. No. 31491) from the Nexpa River. This individual has 15 gray-speckled, pale rings mostly two scales in width, immaculate red rings, relatively pale snout, and relatively broad head ring (head damaged).

The specimen on which the record for *schmidti* from Tenacatita Bay, Jalisco, is based (U.M.M.Z. No. 84257) has 16 immaculate, pale rings two to two and one-half scales in width. The red rings are unspotted and more than twice as wide in the middorsal region as the adjacent black rings. The snout is quite pale, with the rostral and internasals almost completely white, and the prefrontals, nasals, loreals, and first two supralabials more than half white. The posterior margin of the

head ring lies one scale behind the angle of the mouth.

Lampropeltis triangulum schmidti is diagnosed by Stuart (1935) as follows:

"1. Greater number of ventrals, 228 to 233 in *schmidti* as compared with 200 to 221 in *nelsoni*.

"2. Much wider yellow bands between the black annuli, at least, 2½ scales wide in middorsal region in *schmidti* as compared to 1 to 1½ scales wide in *nelsoni*. Conversely the red (in life) spaces between the pairs of black annuli are narrower in *schmidti*.

"3. Much lighter snout.

"4. Posterior chin shields always separated."

The characters of the two specimens collected on the "Puritan" expedition are in general agreement with Stuart's description and diagnosis. The ventrals of one number 223, slightly below the previously known minimum, but the other has 231. I have examined four specimens from the Tres Marías, including U.M.M.Z. No. 79510, a paratype of *schmidti* formerly in the British Museum, and U.S.N.M. No. 24684. There are 12 to 15 immaculate pale rings on the body, from two to three and one-half scales in width. The posterior edge of the pale head ring is one to one and one-half scales behind the angle of the mouth. The scales of the snout (anterior to the frontal) are one-half or more pale. The light body rings of one individual were pale cream color in life, whereas the snout and nuchal band were slightly yellower. The red rings are immaculate.

Comparison of insular *schmidti* with the mainland populations discussed above reveals considerable differences between *schmidti* and "*nelsoni*" of the north-coastal region on the one hand, and between *schmidti* and *blanchardi* of Guerrero on the other. The low number of narrow, pale body rings, mottled snout, and narrow head ring readily distinguish north-coastal "*nelsoni*" from *schmidti*. The subspecies of Guerrero is quite different with its black snout, narrow head ring, and black-spotted red rings.

Lampropeltis triangulum schmidti is less easily distinguishable from typical *nelsoni* than from north coastal "*nelsoni*" or from *blanchardi* of the south coastal region. The insular form and *nelsoni* are similar in number of body annuli, immaculate red rings, and width of head ring. The chief differences are in the color of the snout (mottled in *nelsoni*, largely pale in *schmidti*) and width of pale body rings (one and one-half to two and one-half scales in width in *nelsoni*, two to three and one-half in width in *schmidti*). None of the four *schmidti* (including one large adult) has gray flecks in the pale rings, but this color appears in at least some large *nelsoni*, including the type specimen.

In view of the similarity of *schmidti* to *nelsoni*, it is necessary to reject Smith's (1942b) suggestion that *schmidti* is derived from *L. t. blanchardi* rather than from *nelsoni*.

The king snakes of the Tres Marías Islands, in common with several other insular populations of snakes, have more ventral scales than their mainland relatives. The number in six *schmidti* is 228.8, range 223–232. A sample of 19 snakes from the mainland from Sonora to Guerrero averages 215.5, range 210–221. This range is slightly more restricted than that given by Stuart in his diagnosis (200–221), as I have excluded specimens from the eastern part of the range of *nelsoni* on the Plateau.

Separation of the posterior chin shields, mentioned by Stuart as a diagnostic character of *schmidti*, is seen in the two new specimens. The posterior chin shields are usually in contact in mainland snakes but may be separated. I have not made a quantitative survey of this minor character.

The characters of color pattern given as diagnostic of *schmidti* are not wholly confined to snakes of the islands but are duplicated or closely approached in some snakes of the mainland. Relatively broad light body rings are now known to occur in mainland snakes, and, while the extreme width of rings of some Tres Marías specimens is not attained by individuals on the mainland, there is overlap in the ranges of variation rather than the distinct separation that existed in the specimens and data available to Stuart. Similarly, the snout of the specimens from coastal Jalisco and Colima is fully as light as is seen in insular individuals.

The subspecies *schmidti* is worthy of recognition; the problem is whether the name should be restricted to the insular population, in which case the diagnosis would have to be based on the high ventral counts, or whether

mainland snakes with color pattern highly similar to the insular population should be included in the subspecies. In deciding the taxonomic status of the insular populations of other species, I place little emphasis on differences in ventral scale counts. Following the same direction, I feel that *schmidti* should not be recognized as an insular endemic, but should include a mainland population as well. It is noteworthy that Smith and Taylor (1945, p. 84) include the specimen from Tenacatita Bay, Jalisco, in *schmidti*, despite its mainland origin and low ventral count.

Lampropeltis triangulum schmidti is defined by the following characters of pattern: pale body rings 12–17, immaculate, two to three and one-half scales in width middorsally; scales of red rings immaculate, without black tips; pale head ring broad, with posterior margin one to one and one-half scales behind angle of mouth; scales of snout (anterior to frontal) one-half or more pale.

The range of *schmidti* includes the Tres Marías Islands and coastal Jalisco, with definite localities only on María Madre Island and at Tenacatita Bay, Jalisco. Specimens from Colima are similar to *schmidti* in many respects, but have the pale rings heavily spotted with gray, probably indicating intergradation with either *nelsoni* or *blanchardi*, or with both. The range of *schmidti* may extend north to southern Nayarit, but the coastal plain from Nayarit northward is occupied by a distinct form currently referred to *nelsoni*.

Another facet of variation in *Lampropeltis* is worthy of brief mention. This is the apparent concordance of pattern variation in *Lampropeltis* and in the venomous coral snakes, genus *Micrurus*. The king snake of Guerrero, *L. t. blanchardi*, has a black snout and red rings that are heavily spotted with black; in these ways (but of course not in the arrangement of colors in the rings) there is considerable similarity to a coral snake of the same region, *M. nigrocinctus browni*. The coral snake found on the coastal plain and in the foothills of Nayarit, Sinaloa, and southern Sonora is *M. d. distans*, which has broad, immaculate red rings and usually some pale mottling on the snout. The king snake of this region, *L. t. nelsoni*, also has broad, immaculate red rings and pale mottling on the snout. Even the small Sonoran coral snake, *Micruroides euryxanthus australis*, has much wider red rings in the region of geographic overlap with *Micrurus distans*, suggesting mimicry of a larger, dangerously venomous species by a venomous form that is too small to present a danger to most potential predators. The similarity of *Micrurus* and *Micruroides* also might be interpreted as an instance of Müllerian mimicry (Hecht and Marien, 1956).

A study comparing geographic variation in pattern in *Micrurus* and *Lampropeltis* would undoubtedly provide much of interest. Unfortunately, snakes of both genera are collected too infrequently to provide enough material for detailed analysis.

Leptophis diplotropis (Günther)

Ahaetulla diplotropis GÜNTHER, 1872, Ann. Mag. Nat. Hist., ser. 4, vol. 9, p. 25, type locality Tehuantepec, Oaxaca, Mexico.

Leptophis diplotropis, GÜNTHER, 1894 (1885–1902), p. 130. BOULENGER, 1894 (1893–1896, vol. 2), p. 111. Oliver, 1942, p. 9.

Diplotropis diplotropis, STEJNEGER, 1889, p. 69.

Leptophis diplotropis forreri SMITH, 1943, p. 443, type locality Tres Marías Islands. SMITH AND TAYLOR, 1945, p. 91.

Thalerophis diplotropis, OLIVER, 1948, p. 210.

María Madre Island (A.M.N.H. Nos. 78735, 78743).

The two specimens were obtained by purchase on April 6 and 7. These seem to be the first of their species secured on the islands since Forrer obtained the only other two in 1881, and provide the first record for a specific island. One snake was parasitized by the tick *Amblyomma dissimile* Koch.

The subspecies *L. d. forreri* was described by Smith (1943, p. 443), who noted that ventral counts recorded by Boulenger (1894 [1893–1896, vol. 2], p. 111) for two specimens from the Tres Marías were higher than observed in specimens from the mainland (185 and 186, as against 165 to 181 in 30 mainland specimens). Also, Smith observed that the caudal scales were "perhaps usually more numerous (160 to 166 as opposed to 126 to 161)." No other differences between the form of the mainland and the new insular subspecies were given. In his review of the genus *Thalerophis* (=*Leptophis*), Oliver (1948, p. 210) showed that "The maximum ventral count for males from the northern part of the

range on the mainland (extreme western Chihuahua) differs from that for the insular specimens by two ventrals." He concluded that he saw "no basis at present for recognition of the population to which Smith has applied a name but for which he has presented no diagnostic characters."

The two specimens collected on the Puritan-American Museum expedition are a male with 186 ventrals and a female with 195; neither has a complete tail. There is no question that the snakes from the islands consistently have more ventral scutes than are seen in specimens from the mainland, and, though the ranges of variation approach, they do not overlap as far as is known. I agree with Oliver that the subspecies *forreri* should not be recognized, especially as it is based on only a character shown in other snakes to be subject to modification as a result of environmental effects on the developing embryo.

On the mainland, the range of the species extends from southern Sonora to Chiapas in Pacific drainages.

Masticophis lineatus (Bocourt)

Bascanion lineatus BOCOURT, 1890, Mission scientifique au Mexique et dans l'Amerique centrale, vol. 12, pp. 700–701, type locality Mexico.

Zamenis lineatus, BOULENGER, 1893 (1893–1896, vol. 1), p. 388.

Zamenis flavigularis, GÜNTHER, 1894 (1885–1902), p. 121.

Bascanion lineatum, STEJNEGER, 1899, p. 70.

Drymobius boddaertii, SLEVIN, 1926, p. 201 (part).

Masticophis lineatus, ORTENBURGER, 1928, pp. 134–138.

Coluber striolatus MERTENS, 1934, p. 190 (a substitute name for *lineatus*, a secondary homonym of *Coluber lineatus* Linnaeus [=*Lygophis lineatus*]).

Masticophis flagellum striolatus, SMITH, 1941a, pp. 393–394.

Masticophis flagellum variolosus SMITH, 1943, pp. 448–449, type locality María Magdalena Island (in error, María Madre Island; see below), Tres Marías Islands. SMITH AND TAYLOR, 1945, p. 96.

San Juanito Island (A.M.N.H. No. 76216); María Madre Island (A.M.N.H. Nos. 78682, 78683, 78733, 78734, 78741, 78742); María Magdalena Island (A.M.N.H. Nos. 78696, 78721, 78725).

Masticophis lineatus is the only species of snake known from San Juanito Island, where a specimen was taken by Kenneth Stager on April 21, 1955. This active, diurnal species was encountered more frequently than any other snake by members of the Puritan expedition, but was not found on María Cleofas Island during the brief time spent there, nor has it been taken there by other collectors. Its apparent absence, however, may well be the result of inadequate collecting.

The question of the proper specific name for this species involves both biological and purely taxonomic considerations and requires a brief review. The species was originally named *Bascanion lineatus* by Bocourt (1890). Mertens (1934) noted that this name was a secondary homonym of *Coluber lineatus* Linnaeus, and proposed as a substitute name *Coluber striolatus*. In a review of Mexican racers, Smith (1941a) followed Mertens in the use of the name *striolatus*, but treated the form as a subspecies of the widespread *Masticophis flagellum*. In 1943, Smith adhered to the same nomenclature as in 1941 for the mainland populations, but proposed the subspecific name *M. f. variolosus* for the snakes of the Tres Marías Islands. However, in 1945, Smith and Taylor adopted the viewpoint that secondary homonyms need not be suppressed and accordingly reverted to the use of the name *lineatus* for snakes of the mainland, though these were still regarded as subspecifically related to *Masticophis flagellum*. In the same year, Bogert and Oliver (1945) reported *flagellum* and *lineatus* to be sympatric in southern Sonora, where the two species are readily distinguishable, and referred to the two as *Coluber flagellum piceus* and *Coluber striolatus striolatus*. Further confirmation of the specific distinctness of these two forms was given by Zweifel and Norris (1955), but several authors have persisted in treating *lineatus* (*striolatus*) as a subspecies of *flagellum*. Presumably inadequate knowledge of the literature is the reason, for no one has given arguments to refute the evidence of specific distinctness presented by Bogert and Oliver and by Zweifel and Norris.

As the matter stands at present, the snakes of the Tres Marías Islands may be referred to the species *M. lineatus* (Bocourt) or to *M.*

striolatus (Mertens), if the suppression of secondary homonyms is either necessary or worth while. I prefer to follow Smith and Taylor (1945, pp. 5–6) and to retain use of the name *lineatus*.

The status of the insular population as an endemic subspecies remains to be discussed. Smith (1943, p. 448) described *Masticophis flagellum variolosus*, type locality María Magdalena Island, type specimen U.S.N.M. No. 24681. Dr. Doris Cochran informs me (*in litt.*) that the type actually came from María Madre Island, necessitating a correction of type locality. (The mistake evidently stems from incorrect data on a file card.) Two paratypes (U.S.N.M. Nos. 24680 and 24682) came from María Madre and María Magdalena, respectively.

The new insular subspecies was diagnosed by Smith as follows: "As in *M. f. striolatus*, except ventrals 192 to 197 in males, 195–197 in females; lips not notably mottled in adults." Smith's data covering the scutellation were obtained from 35 specimens from the mainland and 13 from the islands. Utilizing published records as well as specimens in the collection of the American Museum, I have ventral counts for 40 specimens from the mainland and 27 from the islands. Sexual dimorphism is slight or absent. The average number of ventrals for 17 mainland females is 189.2 ± 1.2, range 182–202; for 16 males, 187.1 ± 0.9, range 183–195. With little lost in accuracy it facilitates comparisons to pool the samples of males and females in a comparison of insular and mainland populations. The average of 40 mainland specimens (including individuals with sex undetermined) is 188.1 ± 0.7, range 182–202. This may be contrasted with the average of 196.4 ± 0.5, range 192–204, seen in 27 specimens from the islands. The statistical significance of the average difference is obvious.

The reliability of the pattern character ("[no mottling] in *variolosus* adults, while in *striolatus* the upper labials are prominently mottled" [Smith, 1943, p. 448]) is difficult to assess. Two large insular specimens in the collection of the American Museum conform to Smith's diagnosis of *variolosus*. Among specimens from the mainland, the intensity of mottling varies considerably, though none of the several I have examined is quite so nearly uniform as the insular specimens. The paler mainland specimens show much less distinct mottling than is seen in the specimen illustrated by Ortenburger (1928, pl. 25, fig. 3) to which Smith refers. Juveniles of both mainland and island populations have heavily mottled lips.

The decision concerning recognition of an insular subspecies is perhaps more arbitrary in *Masticophis lineatus* than in other snakes of the Tres Marías. Differentiation in number of ventral scales alone is not an adequate basis for the recognition of an endemic insular subspecies. Whether *variolosus* should be recognized or not depends on the significance attached to the slight but possibly consistent difference in lip pattern, in the apparent absence of more consistent differences. To recognize the subspecies would place undue emphasis on slight variation in a species not otherwise subject to variations sufficiently consistent for it to be considered polytypic, unless it proves to be conspecific with *M. mentovarius*. Hence, *variolosus* should be relegated to the synonymy of *lineatus*.

Larger individuals of *Masticophis lineatus* on the Tres Marías Islands are brownish gray above, with black scale tips and a distinct reddish tinge to the head and neck. The ventrals and subcaudals are white or cream, with brown markings on infralabial and gular scales. The color and pattern are identical with those seen in specimens from the mainland.

A small specimen from María Madre Island had eaten an *Anolis*. The tick *Amblyomma dissimile* Koch was found on *Masticophis*.

On the mainland, *Masticophis lineatus* ranges from southern Sonora to Guerrero and Puebla. To the south and on the east coast it is replaced by *Masticophis mentovarius* (Guerrero and San Luis Potosí to South America), with which *lineatus* conceivably may be conspecific.

Oxybelis aeneus auratus (Bell)

Dryinus auratus BELL, 1825, Zool. Jour., vol. 2, pp. 324–326, type locality "Mexico."

Dryiophis acuminata, GÜNTHER, 1895 (1885–1902), p. 126.

Oxybelis acuminatus, BOULENGER, 1896 (1893–1896, vol. 3), p. 193. STEJNEGER, 1899, p. 69. SLEVIN, 1926, p. 201. SMITH, 1943, p. 458. SMITH AND TAYLOR, 1945, p. 102.

Oxybelis aeneus auratus, BOGERT AND OLIVER, 1945, pp. 381–392.

María Madre Island (A.M.N.H. Nos. 78675, 78744); María Magdalena Island (A.M.N.H. Nos. 78716); María Cleofas Island (A.M.N.H. No. 78731).

This species has been known from the Tres Marías from a specimen collected by Forrer but without data as to which island, and from two specimens collected on María Madre by Nelson and Goldman and by Slevin. The specimens in the American Museum from María Madre were obtained by purchase. Those from María Magdalena and María Cleofas, which represent new insular records, were picked up in dried, skeletonized condition.

Oxybelis aeneus shows comparatively little variation over its great geographic range from Arizona to South America, and only two subspecies are recognized: *O. a. aeneus* in Central and South America, and *O. a. auratus* to the north of the Isthmus of Tehuantepec. Hence it is not astonishing that the insular specimens show no obvious differentiation from those of the mainland. The average number of ventral scales in four specimens from María Madre, 192.5, is very close to the average of 190.24 ± 1.24 determined by Bogert and Oliver (1945, p. 384) for a sample of 33 specimens from Mexico and the United States.

The color in life of a specimen from María Madre was recorded in my field notes: "Dorsal color dark brownish gray. The anterior edges of the dorsal scales of the anterior half of the body are yellow, but the color shows only when the skin is spread. The ground color of the lateral surfaces is slightly paler than the middorsal region and has spots of the darker dorsal gray. Black marks follow the edges of some lateral scales. Ventrals gray with darker spots of brownish gray and a faintly discernible mid-vertebral yellowish gray line."

Both individuals threatened, with the mouth held widely agape, exhibiting the black lining.

Tantilla calamarina Cope

Tantilla calamarina COPE, 1866, Proc. Acad. Nat. Sci. Philadelphia, p. 320, type locality Guadalajara, Jalisco (probably in error, Zweifel, 1959b).

Arroyo Hondo, María Madre Island (A.M.N.H. No. 78745).

The single specimen was found on April 7 in an insect channel in a log resting on moist sand by the stream. The species has not previously been recorded from the Tres Marías Islands; on the mainland it ranges from southern Sinaloa (Mazatlán) southward along the coast to Michoacán and eastward along the edge of the Plateau to Puebla (Smith, 1942a, p. 35).

The specimen is a male, length snout to vent 124 mm., tail length 24 mm. (complete). There are 117 ventrals and 31 paired subcaudals. The number of ventrals is slightly fewer than the minimum of 119 reported by Smith (*loc. cit.*). In life, the snake was pale gray beneath and brown above. There is a relatively weak, dark brown, middorsal line that is widest and most intense on the neck and fades into a series of disconnected dots on the posterior part of the body. On the neck, the line covers the central row of scales and half of each adjacent row, but shortly anterior and posterior to this it narrows abruptly. On the body, dark pigment is confined to the central half of the median row and the tips of the adjacent rows. The stripe narrows on the two scales immediately behind the parietals. The lateral stripe on the third and fourth scale rows is represented over most of the body by a series of short dashes of brown pigment on adjacent halves of the scale rows. Only on the neck do the marks on consecutive scales tend to form a continuous stripe, and even there the stripes of the two scale rows do not fuse to form a single line. These lateral lines are continuous through the temporal region with the dark brown of the top of the head. On the nape and posterior edge of the parietals there is a pale, crescentic marking broken medially by the narrow anterior prolongation of the central stripe.

In some respects this specimen differs from the description of the species given by Smith (*loc. cit.*). The median stripe is constricted on the neck, rather than spreading over the top

of the head, though there is continuity between the stripe and the dark brown pigment of the head. The lateral stripes are continuous with the dark color of the head rather than being separated. The snake was various shades of brown or gray-brown above, and pale gray beneath, rather than light gray above and white below. Smith's description may be based on preserved specimens, but field notes accompanying a specimen (A.M.N.H. No. 19750) from the Distrito Federal state that it was "gray, with white abdomen."

The specimen from the Tres Marías has been compared with six specimens in the collection of the American Museum from Nayarit, Colima, and Distrito Federal. In these mainland specimens, the stripes are generally broader and better defined than in the insular specimen. The median stripe expands on the nape, as described by Smith, or is only slightly constricted. There is no suggestion of a crescentic pale marking on the nape. On the insular specimen, this marking results from the abrupt constriction of the median line and from the presence of two short but distinct additional dark lines on each side of the neck between the lateral and median lines. These short lines, which are only faintly indicated in specimens from the mainland, separate the light lateral field from the mark on the neck. Specimens from the mainland have the lateral field essentially continuous forward to the posterior edge of the parietals.

It should be evident from the foregoing comparison of color pattern in insular and mainland specimens that the single individual from the Tres Marías Islands differs from the specimens with which it was compared. In the absence of an adequate number of specimens from the islands or the mainland, the significance of the differences cannot be assessed, although a lower order of differentiation similar to that seen in some other snakes of the islands may be suspected.

Pelamis platurus (Linnaeus)

Anguis platura LINNAEUS, 1766, Systema naturae, ed. 12, p. 391, type locality Pine Island, Pacific Ocean.

Pelamydrus platurus, SLEVIN, 1926, p. 202.

The yellow-bellied sea snake is known on the Tres Marías Islands only from a dead specimen found on the beach of María Magdalena (Slevin, 1926, p. 202). It is at times locally abundant in the waters of western Mexico. For example, Paul D. Rüthling collected 13 of these snakes on February 7, 1920, about 15 miles offshore between Mazatlán, Sinaloa, and San Blas, Mayarit, and on February 10 collected 18 more south of Puerto Vallarta, Jalisco (specimens in the American Museum of Natural History collection).

Agkistrodon bilineatus bilineatus (Günther)

Ancistrodon bilineatus GÜNTHER, 1863, Ann. Mag. Nat. Hist., ser. 3, vol. 12, p. 364, type locality Pacific coast of Guatemala; 1895 (1885–1902), p. 186. BOULENGER, 1896 (1893–1896, vol. 3), p. 522.

Agkistrodon bilneatus, STEJNEGER, 1899, p. 71. GLOYD AND CONANT, 1943, p. 163.

This species, the only dangerously venomous snake known on the islands, was not encountered by the Puritan-American Museum expedition. It is known from the Tres Marías Islands from two specimens collected by Forrer on the "Tres Marías" and one obtained by Nelson and Goldman on María Madre Island. The Mexican moccasin ranges widely on the mainland, from southern Sonora to Yucatan and Nicaragua. An apparently isolated population in Tamaulipas has been given the name *A. b. taylori* by Burger and Robertson (1951); otherwise, the species is regarded as constituting a single form. Ventral counts given in the literature for the three specimens from the Tres Marías (137, 138, and 141) are close to the average for the species as a whole, 135 scales, and fewer than the maximum of 144 scales (Gloyd and Conant, 1943, p. 168). *Agkistrodon* does not appear to share with several other insular populations their tendency to increase the number of ventral scales.

ZOOGEOGRAPHY AND TAXONOMY

GEOLOGIC HISTORY OF THE TRES MARÍAS ISLANDS

GEOLOGIC HISTORY is a matter of prime interest in a study of insular biogeography. It is desirable to have as complete a knowledge of the geology as possible, if reliable inferences are to be made concerning connections with the mainland and the period of existence of land masses. Unfortunately, the geology and paleontology of the Tres Marías are relatively poorly known. Most of the information was obtained by the California Academy of Sciences expedition in 1925 and is contained in papers by Hanna (1926 and 1927), Hanna and Grant (1926), and Jordan and Hertlein (1926). Additional data are provided by Hertlein and Emerson (1959).

María Madre Island is the best known. On the north and east sides of the island, Pliocene limestones and sandstones, up to 400 feet in thickness, are underlain by upper Miocene diatomaceous shales about 1000 feet thick. These shales in turn are underlain by diorite and then granite. The lowlying southern end of the island appears to be an elevated Pleistocene beach (Hanna, 1927). There is evidence suggesting the presence of a land mass in the position of the Tres Marías in the Pliocene: "This whole mass was land during part of the Pliocene because many boulders of granite are in the sediments of that age" (Hanna, 1926, p. 69). The land may have been peninsular or even insular. Hanna (*loc. cit.*) states, "During a portion of Pliocene time large coral reefs existed around this old land mass." The reef exposures observed by Hanna are on the northern and eastern sides of the island, so it cannot be assumed that the land mass was surrounded by reefs, as the use of the word "around" might be taken to indicate. The sea bottom slopes quite abruptly on the oceanic side of the Tres Marías (fig. 1). Though this steep slope may in part be due to post-Pliocene movements, it seems unlikely that any major land mass existed to the west of the present position of the islands. This, together with the known presence of coral reefs on the eastern side of María Madre, suggests that the Pliocene land area may have been peninsular or even insular.

In his brief survey of María Magdalena Island, Hanna (1927, p. 23) found "no evidence . . . of the great deposits of Pliocene and Miocene organic shales and limestones. The two islands [Madre and Magdalena] have entirely different geological histories." Hertlein and Emerson (1959), however, reported the presence on María Cleofas (an island that Hanna did not visit) of mid-Pliocene deposits correlating with those described on María Madre by Hanna. It may be that a more extensive survey of María Magdalena would explain the anomaly.

The presence of marine deposits of Pleistocene age on the three larger islands indicates that during at least part of the Pleistocene the area above water was somewhat reduced. Tiny San Juanito Island may have been submerged, but nothing is known of its geology.

An important question is when the islands may last have been connected with the mainland. The nature of the herpetofauna strongly indicates that there was such a connection, but geological information offers no clue to dating. It is generally agreed by geologists that during glacial maxima enough water was locked up in continental glaciers to cause a marked world-wide lowering of sea level. Estimates of the magnitude of the effect on sea level vary widely, but many geologists accept a lowering of from 350 to 450 feet as representing the probable maximum effect at the time of most extensive glaciation. Of course, local crustal movements could add to or subtract greatly from this figure, especially in an area as active tectonically as western North America.

It is of interest to determine the effect that a lowering of the sea level 350 to 450 feet would have on the isolation of the Tres Marías under present conditions of sea-bottom topography. The shoreline of the shrunken sea would fall between the 50- and 100-fathom contours (fig. 1). The islands

would still be separated from the mainland by a distance of 15 to 20 miles (as opposed to the present minimum distance of about 50 miles), with a minimum depth of over 800 feet of water in the intervening gulf. As incidental effects, there would probably be some interconnections between islands, and a new island would be formed between María Cleofas and Punta Mita. Dr. Robert Fisher informs me (*in litt.*) that the minimum depth of the submarine elevation between María Cleofas and Punta Mita is 35 fathoms.

It is evident that a lowering of the sea level 350 to 450 feet would not establish a dry-land connection between the islands and the mainland, though it would reduce the size of the water gap and thus facilitate rafting. If the estimate of maximum lowering of the sea level is even approximately correct, crustal movements must have played an important part in the formation of the Tres Marías Islands. The differential movement of 800 to 1200 feet needed for a dry-land connection to be formed is of a magnitude similar to the displacement that is thought to have occurred in Pleistocene time in other parts of western North America. For example, Woodring *et al.* (1946) consider the highest marine terrace in the Palos Verdes Hills near Los Angeles in southern California, which is some 1200 feet above sea level, to be upper Pleistocene in age.

In passing, it is noted that Isabel Island, which is volcanic in origin, lies in shallow water and, if in existence during a period of lower sea level, would have been an isolated hill on the coastal plain.

To summarize, the meager geologic evidence suggests that there may have been dry land in the region of the present Tres Marías Islands since mid-Pliocene. It is uncertain when this area may have been insular and when it was part of the mainland. Glacial lowering of the sea level would not suffice to connect the islands with the mainland; crustal movement must also have occurred if the islands once were part of the mainland.

TAXONOMY, ENDEMISM, AND SPECIATION

There is no generally acceptable formula for the taxonomic allocation of insular populations, as each case must be considered for itself. There are, however, trends of opinion among biologists that markedly influence taxonomic decisions. One viewpoint seems to be that physical isolation imposed by the insular habitat is the most important factor, and any slight morphological differentiation combined with this isolation provides sufficient justification for separate taxonomic recognition. Hence, insular subspecies often represent a degree of differentiation that, in a population of the mainland, would not be considered adequate reason for the application of a subspecific name. Similarly, species endemic to islands sometimes appear to be the equivalent of subspecies on the mainland.

A more conservative treatment regards insular populations as subspecies whenever the parental stock on the mainland is obvious, and the degree of differentiation in not vastly different from that seen among various populations on the mainland. Minor variation is certainly worthy of attention but need not be given the emphasis of formal taxonomic recognition. Of course the problem of deciding what constitutes major and minor variation remains subjective.

The herpetological literature includes numerous instances of divers opinions on taxonomic allocation of insular populations. As an example, the salamander *Triturus ensicaudus* of the Riukiu Islands (assigned to the genus *Cynops* in recent literature; I use *Triturus* merely to conform to the older papers to which I refer) is clearly related to *T. pyrrhogaster* of Japan and was considered a subspecies of *pyrrhogaster* by several authors. Other persons accord it the status of a species endemic to the Riukiu Islands. In a review of the amphibians of the Riukiu Islands, Inger (1947) treated *ensicaudus* as an endemic species and divided the insular populations into two subspecies. The form newly named, *T. e. popei*, was diagnosed as differing from typical *ensicaudus* "in that almost half of the individuals have light cream or yellow spots in the mid-dorsal region" (*supra cit.*, p. 319). This may be cited as an example of minor

variation. Evidently less than half of the population would be referable to subspecies unless geographic criteria were employed.

Hybridization of *Triturus ensicaudus* and *T. pyrrhogaster* was reported by Kawamura (1950), who found that, although the species differ genetically, not only are viable hybrids produced, but the hybrids are fertile. He concluded that *ensicaudus* is a subspecies of *pyrrhogaster*. Hence, in the case of these salamanders, we have an example of a form that has been considered as (1) an endemic, polytypic species, (2) an endemic, monotypic species, and (3) a subspecies of a more wide-ranging form.

The taxonomic treatment of the herpetofauna of the Tres Marías adopted here differs from that of previous authors. Smith and Taylor (1945) consider six of 10 snakes known on the islands as endemic species or subspecies. In comparison, I recognize only two endemic forms among these 10 and add one species, non-endemic, to the fauna. This relatively great change from a snake fauna that is considered 60 per cent endemic to one only 18 per cent endemic requires explanation.

First, the apparently endemic genus and species *Exelencophis nelsoni* may be dismissed. The complete lack of material of this lost species prohibits an assessment of its position, although I will be surprised if it proves to be an endemic species, much more so if an endemic genus.

One form that is thought to be an insular endemic by its describer, *Lampropeltis triangulum schmidti* Stuart, was reported from the mainland by Smith and Taylor (1945, p. 84), and this report is confimed and amplified here (pp. 104–107). *Dryadophis melanolomus slevini* is treated as an endemic here and also by Smith and Taylor. There remain four forms (36% of the snake fauna) that are considered by Smith and Taylor to be endemic subspecies but that I prefer to include in the same subspecies as mainland populations. One of these (*Drymarchon*) was named by Brock in 1942; the others (*Boa*, *Masticophis*, and *Leptophis*) were named by Smith in 1943.

The insular forms about which there is disagreement have one diagnostic feature in common: all have more ventral scales than their mainland relatives. Only one, *Masticophis*, has a slight difference in color pattern that may help to distinguish it from snakes of the mainland; the others are virtually identical with mainland populations.

The ventral scale counts of snakes of the Tres Marías are summarized and compared with those of mainland samples in table 1. It is evident that acquisition of more material since the insular forms were named has not erased distinctions noted by the describers. The problem is whether, in the absence of other well-defined differentiation, a difference in ventral counts is sufficient reason for subspecific recognition. Modern taxonomic prac-

TABLE 1

VENTRAL SCALE COUNTS OF SNAKES FROM THE TRES MARÍAS ISLANDS AND MAINLAND[a]

Species	Islands			Mainland		
	Mean	Range	*N*	Mean	Range	*N*
Boa constrictor	257.0	253–260	9	241.6	225–253	61
Oxybelis aeneus	192.5	190–195	4	190.2	174–204	33
Dryadophis melanolomus	♂184.2	182–187	4	♂179.8	179–185	10
	♀188.7	186–190	4	♀185.1	180–190	11
Masticophis lineatus	196.4	192–204	27	188.1	182–202	40
Drymarchon corais	203.0	200–209	9	194.7	190–201	27
Lampropeltis triangulum	228.8	223–232	6	215.5	210–221	19
Leptophis diplotropis	♂185.6	185–186	3	♂174.4	167–184	37
	♀195	195	1	♀178.0	172–184	23
Imantodes gemmistratus	253+	253+	1	227.1	220–231	6
Tantilla calamarina	117	117	1	—	119–132	6
Agkistrodon bilineatus	138.7	137–141	3	135	129–144	46

[a] Sources of these data are given in the respective species accounts.

tice is to recognize and classify genetic differences between populations, but in the vast majority of cases the genetic determination of characters that are utilized by the taxonomist necessarily is inferred rather than demonstrated experimentally. Undoubtedly, the limits of variation in ventral scales (body segments) are genetically determined, but Fox (1948) demonstrated that the scutellation of ovoviviparous garter snakes is modified by the temperature at which gravid females are kept. This should instill caution in the recognition of subspecies based solely on differences in ventral counts. That insular populations of snakes tend to have higher average ventral counts than their mainland relatives is well known (Mertens, 1934). Recognition of subspecies based on differences in ventral counts, without the concurrence of other distinctive characters, places undue emphasis on variation possibly not determined genetically.

Of the remaining amphibians and reptiles recorded from the islands, only one (*Cnemidophorus*) has been considered an endemic form. It was described as *Cnemidophorus mariarum* by Günther [1885 (1885–1902)], treated as a subspecies of *C. sacki* by Smith and Taylor (1950), and called a subspecies of *C. communis* in the most recent revision (Zweifel, 1959a).

Islands are looked upon as natural laboratories for the study of speciation. On the one hand, islands usually have more uniform climatic conditions than comparable continental areas. Such a uniformity sometimes allows the persistence on islands of forms exterminated or even extinct on the mainland. Also, the isolation imposed on the insular habitat protects the fauna from competition with recently evolved and perhaps more aggressive and successful mainland types. While climatic stability and isolation may retard evolutionary progress on islands, on the other hand there are factors that may promote differentiation. Given the relatively slight diversity of habitat on an island, there is less room, ecologically speaking, for species with similar ecologic niches. Competition may eliminate the less well-adapted species and promote selection of better-adapted genotypes among surviving forms. Climatic change following insular isolation may exterminate the less adaptable members of the fauna and simultaneously stimulate evolutionary changes in survivors.

There appears to be relatively little evolutionary divergence of the herpetofauna with respect to the parental mainland stocks. The only endemic subspecies, *Cnemidophorus communis mariarum* and *Dryadophis melanolomus slevini*, are representatives of southern species not known to occur today as far north as the latitude of the islands. Presumably at the time these species reached the islands, a slightly moister climate prevailed, in keeping with the conditions on the mainland where they exist today. Evolutionary change may be correlated with the development of the relatively more arid climate that appears to prevail on the islands, though it is difficult to see any relationship between climate and the characters of color pattern that distinguish the insular subspecies from mainland populations.

The ranges of *Cnemidophorus sacki* and *C. communis* are, as far as known, allopatric, with *sacki* found in more arid regions. On this ecological basis, one would expect to find *sacki* rather than *communis* on the islands. Possibly the separation of the islands from the mainland has prevented replacement of *communis* by *sacki* as conditions become more arid.

The low degree of insular endemism may indicate that the islands are of relatively recent date, or this may reflect the conservative nature of reptile and amphibian evolution. As fossils of small reptiles and amphibians are studied more intensively, the number of recent species recorded from Pleistocene, Pliocene, and even earlier deposits continues to grow. The absence of strong differentiation in the insular fauna is not conclusive evidence of recent isolation, though Mertens (1934, p. 36) was led to suggest that Isabel and the Tres Marías Islands were perhaps formed in the Quaternary period. Similarly, Stejneger (1899, p. 63) inferred "a comparatively recent severance of the islands from each other as well as from the opposite mainland of Mexico."

The low degree of endemism in the herpetofauna is in marked contrast to the situation in birds and mammals, judging by taxonomy currently in use. All five land mammals are

recognized as endemics. Three of these are given specific status (*Procyon insularis*, *Oryzomys nelsoni*, and *Sylvilagus graysoni*), and two subspecific (*Marmosa canescens insularis* and *Peromyscus boylii madrensis*). Different subspecies of *Procyon insularis* are recognized on María Madre and María Magdelena Islands (Hall and Kelson, 1959).

A list of the birds of the Tres Marías is given by Stager (1957, pp. 428–430). Thirty-six species of land birds are recorded as breeding on the islands; 25 of these are endemic subspecies. The disparity in relative number of endemic forms of endotherms and ectotherms may reflect differences in evolutionary rates, but may result in part from a finer degree of splitting by students of birds and mammals.

GEOGRAPHIC RELATIONSHIPS OF THE HERPETOFAUNA

The geographic relationships of the fauna are shown in figures 3 and 4. The map was made by superimposing distribution maps for the species known from the Tres Marías and illustrates in a general way the species density on the mainland of members of the insular fauna. Only those portions of the ranges that lie within Mexico (including Baja California) are shown. Certain species are not represented on the map: marine species are, of course, excluded; the crocodile is omitted because of its obvious aquatic dispersal; *Exelencophis nelsoni*, known only from the islands, is not mapped. There remain 18 species of amphibians and reptiles common to the islands and mainland. As far as known, no more than 16 species of the island fauna occur together on the mainland owing to the failure of some northern and southern forms to overlap. The area of maximum density is in Colima and adjacent Jalisco.

Herpetologists familiar with the taxonomy and distribution of amphibians and reptiles of western Mexico will realize that a map such as this must necessarily be constructed on a base of inadequate knowledge. The distributions of even the commonest species are poorly known. Also, alteration of the taxonomic status of a given form could result in rather impressive changes in the density map. As examples, we may consider the following species: The gecko *Phyllodactylus lanei* is thought to range from Sinaloa to Guerrero. It may be conspecific with forms ranging from central Sonora (or even southern California) to Central or South America. *Masticophis lineatus* is found from southern Sonora to Guerrero, but may belong to the species *M. mentovarius* which is known from San Luis Potisí and Guerrero to South America. *Cnemidophorus communis* is restricted to western Mexico, but may belong to a species represented as far south as Honduras. At the other extreme, the wide-ranging turtle *Kinosternon integrum* may be a composite of two or more species.

The map emphasizes the expected similarity of the insular fauna to that of the adjacent mainland. More significant is the pronounced evidence of affinities with mainland populations to the south. The islands have as many species in common with Yucatan as with south-central Sonora, and (although the map does not extend far enough south to show this) as many species in common with northern South America as with central Sonora. The lack of any species in common with Baja California is notable. Another point to be mentioned is the preponderance of lowland species in the fauna of the islands. The only two species common to the islands and the southern part of the Mexican Plateau are the widely distributed and evidently adaptable king snake (*Lampropeltis triangulum*) and mud turtle (*Kinosternon integrum*).

There are two species of reptiles that, as far as is presently known, have their northern outpost on the Tres Marías Islands. These are the whiptail lizard, *Cnemidophorus communis*, and a racer-like snake, *Dryadophis melanolomus*. Perhaps significantly, these are the only two species represented on the Tres Marías by endemic subspecies. *Cnemidophorus communis* is found on the mainland at Chamela Bay, Jalisco, 140 miles southeast of María Cleofas and 90 miles from the point of land nearest to the islands. The mainland of Nayarit opposite the Tres Marías is inhabited by a related species, *C. sacki*. Neither

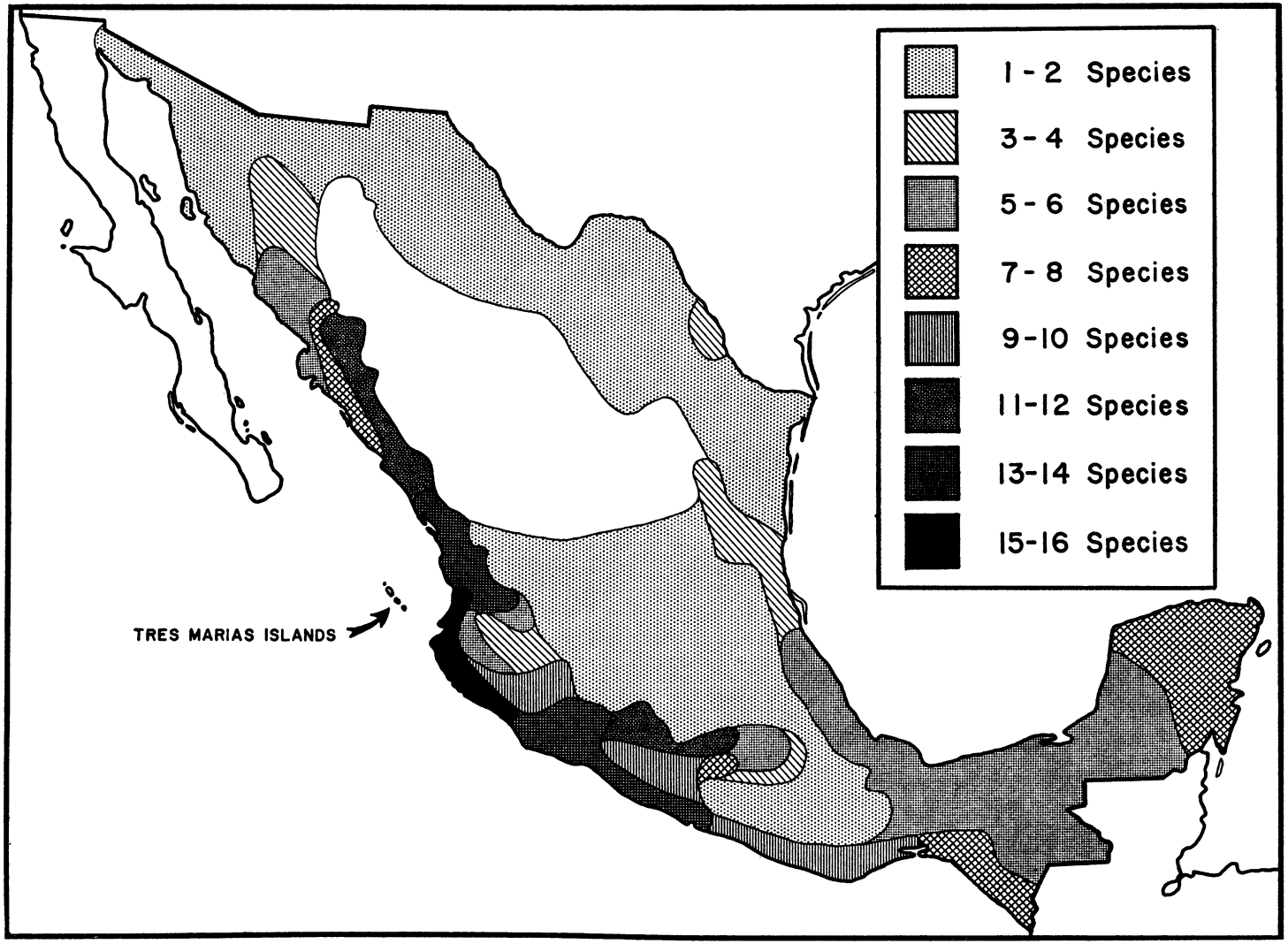


FIG. 3 Species density on the mainland of Mexico (including Baja California) of amphibians and reptiles found on the Tres Marías Islands. The number of insular species believed to inhabit a particular area on the mainland is indicated by the shading pattern.

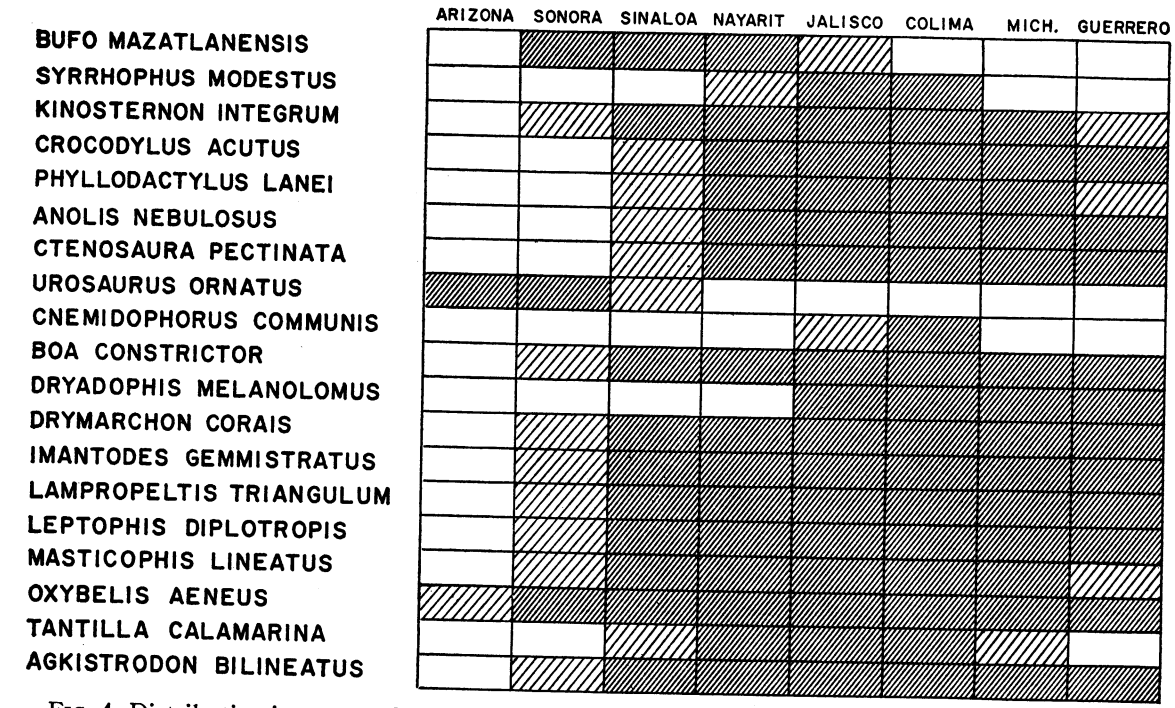


FIG. 4. Distribution in western Mexico of the species comprising the herpetofauna of the Tres Marías Islands. Dark shading indicates that the species concerned is found through all or most of the western part of the state; light shading indicates a range that terminates well within the state; and the absence of shading implies the absence of the species. For example, *Bufo mazatlanensis* is not known from Arizona, but ranges from northern Sonora through Sinaloa and Nayarit, barely reaching into Jalisco.

sacki nor *communis* has yet been found at Banderas Bay, but *sacki* occurs in southern Nayarit and hence closer than *communis*. *Dryadophis* is known from Puerto Vallarta on Banderas Bay, about 80 miles southeast of María Cleofas, but has not been found so far north as the coast of Nayarit opposite the islands. A similar pattern of distribution is seen in the parrot, *Amazona ochrocephala tresmariae* Nelson. The insular population represents an endemic subspecies of a species known on the mainland no farther north than Colima (Stager, 1957, p. 422).

Although most species of the island fauna range both north and south of the islands, there are two that are northern in distribution and deserve special mention. *Bufo mazatlanensis* ranges from northern Sonora to Banderas Bay and thus has almost all of its distribution to the north of the islands. It is apparently closely related to several species (the "*valliceps*" group) of eastern and southern Mexico and Central America. The only link connecting *mazatlanensis* geographically with the toads of southern Mexico is *Bufo gemmifer*, known from a single locality in Guerrero, and collecting in Colima and Michoacán has yielded no toads of this group. *Bufo mazatlanensis* appears to be a northern disjunct of an essentially southern group of toads, but also might be thought of as a trans-plateau disjunct.

The lizard *Urosaurus ornatus* is unique in that it is the only species on the islands that is not found on the mainland at least as far south as northern Jalisco. The species ranges widely over the southwestern United States and northern Mexico (fig. 5). It is common in southern Sonora, where its range overlaps that of a southern relative, *U. bicarinatus*. The form of the Tres Marías Islands, *U. o. lateralis*, was described by Boulenger from specimens collected by Forrer on the Tres Marías and in southern Sinaloa at Presidio, near Mazatlán. This is the same subspecies that occurs in northern Sinaloa and southern

Sonora. Although considerable collecting has been done in the region of Mazatlán, no additional records for this lizard in southern Sinaloa have been published during the 70 years since *lateralis* was described. The southernmost record verifiable is Culiacán, 140 miles northwest of Presidio and 220 miles from the Tres Marías (A.M.N.H. No. 62346). *Urosaurus ornatus* is usually common and easily collected where it occurs, so its absence in collections from southern Sinaloa suggests that it truly is not present there. Possibly a specimen collected by Forrer on the Tres Marías was erroneously labeled as coming from Presidio, where he also made large collections.

As discussed in the species account, there exists an anomaly in the distribution of *Urosaurus* on the islands. The lizard is found on the three northern islands, but apparently not on the southernmost, María Cleofas. Topographic relationships of the islands, the

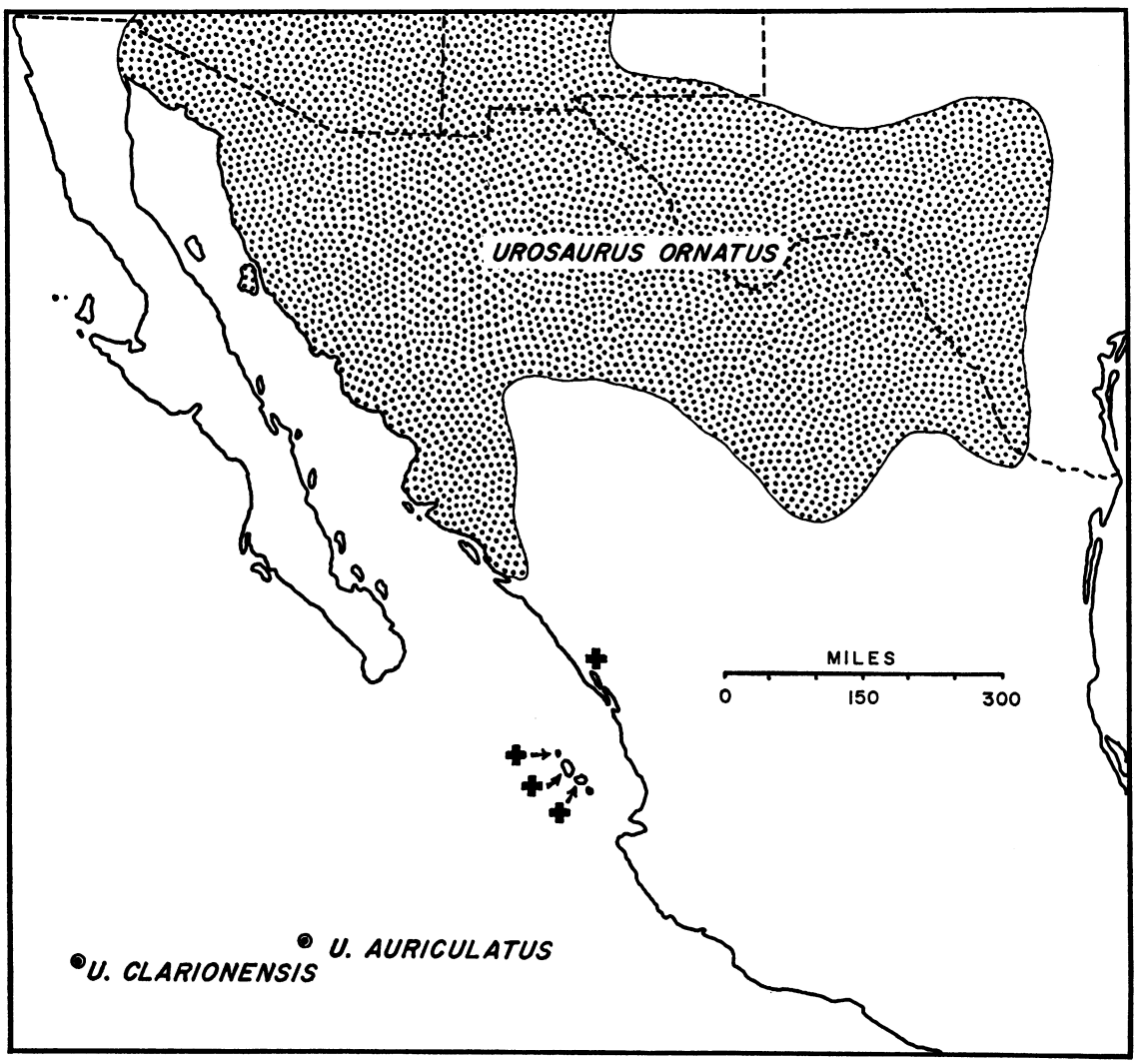


FIG. 5. Distribution of *Urosaurus ornatus* and related species. Crosses indicate the three islands of the Tres Marías upon which *ornatus* is found, and a single possibly questionable locality on the mainland (Presidio, Sinaloa). Related species on Clarion and Socorro Islands are mapped. Several subspecies are recognized within the range of *ornatus;* the insular form is *U. o. lateralis*, the same subspecies that occupies the southwestern corner of the range on the mainland.

mainland, and the surrounding sea bottom suggest that the islands may once have been part of a peninsula extending northwestward from Punta Mita (fig. 1). If *Urosaurus* reached the islands by such a land connection, it would be expected to be present on María Cleofas if on the other islands. The apparent absence of *Urosaurus* from María Cleofas, together with the absence of the species from the adjacent mainland, suggests that this species may have reached the islands by over-water dispersal from the north. This could have happened at a time when the three northern islands formed one continuous land mass, while María Clefoas stood separate, and may explain the present insular distribution. In this connection, it is noted that the channel between María Cleofas and María Magdalena is about twice the width of that separating María Magdalena and María Madre.

The question of potential for over-water dispersal by *Urosaurus* arises and can be answered in the affirmative. On the volcanic and unquestionably oceanic Revillagigedo Islands, more than 200 miles from the nearest land, there are two species of *Urosaurus:* on Clarion Island, *U. clarionensis*, and on Socorro Island, *U. auriculatus*. These species are thought to be most closely related, respectively, to *Urosaurus ornatus* and *Urosaurus bicarinatus* of western Mexico (see Brattstrom, 1955, and Mittleman, 1942, for discussion).

The ecological position of *Urosaurus* on the Tres Marías Islands also bears on this discussion. On the mainland, this species characteristically inhabits elevated situations, being found most often on tree trunks and rocks. On the islands it appears to be restricted largely to the beach and adjacent low forest, whereas *Anolis nebulosus* inhabits the arboreal and rocky situations. The inference is that *Urosaurus* reached the islands as a late-comer and, with arboreal and rocky habitats preëmpted by a possible competitor, successfully occupied a habitat somewhat foreign to its place on the mainland.

The argument that *Urosaurus* reached the islands by dispersal over water does not necessarily extend to the rest of the herpetofauna. On the contrary, the remaining species (*Crocodylus* is an exception) presumably represent the residue of a fauna isolated by the diastrophic movements and sea-level changes that formed the Tres Marías Islands.

Evidence for this comes from several sources. Though it is known that anurans sometimes successfully cross salt water from mainland to island, or island to island (see Myers, 1953, for an illuminating discussion), the presence of frogs on islands suggests a former land connection, especially if this interpretation is not at variance with inferences based on the composition of the rest of the fauna. On the Tres Marías we have *Syrrhophus* and *Bufo* and almost certainly other species of frogs not yet collected.

The fresh-water turtle of the islands, *Kinosternon*, might conceivably survive a journey through the ocean, but the scarcity of suitable habitat on the islands would seem to render an effective landfall extremely unlikely. The fauna of an oceanic island characteristically includes many more species of lizards than of snakes. Such a disparity is evidently a consequence of the greater potential lizards have for over-water dispersal. The ratio of species of lizards to snakes in the fauna of the Tres Marías is 5/11 which is similar to that estimated for the coastal region of Jalisco, 18/33. There is no indication here of the imbalance often seen in an oceanic fauna.

An old oceanic fauna may show considerable diversity traceable to the radiation of a few migrant stocks. The herpetofauna of the Tres Marías shows little evidence of adaptive modification *in situ*, and the species (excluding the puzzling *Exelencophis*) are morphologically identical or highly similar to mainland populations.

There appear to be only five species of land mammals (excluding bats) native to the Tres Marías. This poverty might imply the lack of any previous connection with the mainland. However, mammal faunas characteristically suffer relatively greater depletion on small islands than does the herpetofauna. For example, South Coronado Island off the northern coast of Baja California has 10 species of amphibians and reptiles but only a single mouse. Santa Cruz and Santa Catalina Islands off southern California have,

respectively, four and five native land mammals, as against 10 and 11 amphibians and reptiles.

The presence of a fresh-water fish, *Agonostomus nasutus*, on María Cleofas and María Magdalena (Nelson, 1899) is of questionable zoogeographic significance, as the larval stage of an *Agonostomus* (not the species on the Tres Marías) is known to occur in the ocean (Anderson, 1957).

Isabel Island (fig. 1) does not belong to the Tres Marías Group and has no direct faunal relationship with it. The fauna is known to include only four species of reptiles and no amphibians. A single snake, *Lampropeltis triangulum nelsoni*, is present. The same form inhabits the coastal plain of Nayarit and Sinaloa, in contrast to typical *nelsoni* of the highlands (see p. 104) and *schmidti* of the Tres Marías. The lizards, too, are species found on the adjacent shore. *Ctenosaura pectinata* is common to the mainland, Isabel Island, and the Tres Marías, but *Sceloporus clarki boulengeri* and *Cnemidophorus sacki huico* do not occur on the Tres Marías.

Geologic evidence offers no clue as to when the Tres Marías Islands may have been severed from the mainland. One other possible method of dating suggests itself. It is generally assumed that South America was isolated from Middle America throughout most of the Tertiary, with the land bridge established late in the Pliocene. Four species of snakes on the Tres Marías are also found in South America. If any of these could be shown to be of South American origin, it could be assumed that the disjunction of islands and mainland was no earlier than late Pliocene, and probably more recent, to allow time for migration from South America to western Mexico.

Lampropeltis triangulum and *Drymarchon*

TABLE 2

DISTRIBUTION OF TWENTY-THREE AMPHIBIANS AND REPTILES ON THE TRES MARÍAS ISLANDS

	San Juanito	María Madre	María Magdalena	María Cleofas
Bufo mazatlanensis	—	x[a]	—	—
Syrrhophus modestus pallidus	—	x	x	—
Eretmochelys imbricata	—	—	o	—
Chelonia mydas	o	—	—	—
Kinosternon integrum	—	x	—	—
Crocodylus acutus	—	—	s	—
Phyllodactylus lanei	—	x	x	x
Anolis nebulosus	x	x	x	x
Ctenosaura pectinata	x	x	x	x
Urosaurus ornatus lateralis	x	x	x	—
Cnemidophorus communis mariarum[b]	x	x	x	x
Boa constrictor imperator	—	x	x	x
Dryadophis melanolomus slevini[b]	—	x	x	x
Drymarchon corais rubidus	—	x	x	x
Exelencophis nelsoni[b]	—	x	—	—
Imantodes gemmistratus latistratus	—	x	—	—
Lampropeltis triangulum schmidti	—	x	—	—
Leptophis diplotropis	—	x	—	—
Masticophis lineatus	x	x	x	—
Oxybelis aeneus auratus	—	x	x	x
Tantilla calamarina	—	x	—	—
Pelamis platurus	—	—	o	—
Agkistrodon bilineatus bilineatus	—	x	—	—

[a] *Symbols:* x, presence on island verified by specimens; o, marine species found in adjacent waters or dead on shore; s, sight record only.

[b] Forms endemic to the Tres Marías Islands.

corais are widely distributed north of the Isthmus of Panama, where several subspecies of each have evolved. In contrast, only a single subspecies of *Lampropeltis* and two of *Drymarchon* are found in South America, from which it may be inferred that the species underwent a long period of evolution in Middle America, with comparatively recent migration to South America.

Oxybelis aeneus is composed of two subspecies: *aeneus*, with a range extending from Guatemala to southeastern Brazil, and *auratus* of Mexico and southern Arizona. The center of differentiation for the genus appears to be in South America, but there is no way of knowing where *O. aeneus* originated.

Boa constrictor is the only one of the four species for which there is evidence of a South American origin. A single subspecies ranges from Mexico to northern South America, and four additional subspecies are recognized in South America. Such a small number suggests either inadequate taxonomic treatment of populations north of South America or a period of differentiation in South America and subsequent dispersal northward, but inference based on the distribution of this one species can scarcely be considered adequate for dating the time of separation of the islands.

To summarize, the herpetofauna of the Tres Marías Islands most closely resembles that of the coastal region 75 to 150 miles to the southeast of the islands and shows less similarity to the mainland fauna at the latitude of the islands. One species, *Urosaurus ornatus*, may have become established after over-water dispersal from the north, but the bulk of the fauna probably is composed of descendants of animals isolated when the islands became separated from the mainland. The presence of southern disjuncts on the islands suggests that the islands may have been severed from the mainland at a time when slightly more tropical conditions prevailed.

COMPARISON OF MAINLAND AND ISLAND FAUNAS

As a basis for comparison, I have compiled the following lists of 75 amphibians and reptiles that are presumed to inhabit the coastal region of Jalisco. This region was chosen, rather than Nayarit directly opposite the island, because the presence of northern elements in the fauna of Nayarit would bias the comparison, especially as the insular fauna has such a pronounced southern aspect. The list of species from Jalisco was compiled from published reports, specimens in the American Museum of Natural History, and a list of specimens in the Museum of Zoölogy, University of Michigan, kindly furnished by Dr. Charles F. Walker. The basic published list is that of Smith and Grant (1958) for Puerto Vallarta. Several species not recorded from Jalisco but known to occur to the north and south (Zweifel, 1959c) are included. Many forms on the list probably are not found on the coastal plain but may occur in the foothills near the coast. Species known only from higher elevations have been excluded.

FROGS

Bufo marinus
Bufo marmoreus
Bufo mazatlanensis[1]
Bufo occidentalis
Eleutherodactylus occidentalis
Eleutherodactylus vocalis
Leptodactylus melanonotus
Microbatrachylus hobartsmithi
Syrrhophus modestus[1]
Tomodactylus nitidus
Agalychnis dacnicolor
Hyla baudini
Hyla smithi
Phrynohyas inflata
Pternohyla fodiens
Hypopachus oxyrrhinus
Microhyla usta
Rana pipiens
Rana pustulosa
Rana sinaloae

The list of mainland forms includes 20 species, of which two are known on the islands. The existence of some mainland forms on the islands is ecologically improbable. The three species of *Rana* and *Leptodactylus* seem to require a permanent supply of water more extensive than is furnished by the few small springs and intermittent streams on

[1] Species present on the Tres Marías Islands.

the islands. Of the remaining 14 species, several may be present though undetected. Natives on María Madre Island described a large *sapo* that may have been *Bufo marinus*. Tales of loud summertime choruses of frogs undoubtedly relate in part to *Bufo mazatlanensis*, which produces a penetrating trill, but probably other anurans are involved as well. A shipment of specimens supposedly sent from the Tres Marías, but never received at the American Museum, was reported to contain "6 green toads," probably a species of hylid.

There is little hope of learning more about the anuran fauna until collections are made on the islands during the summer rainy season. A week spent on the islands at the proper time would probably yield more information on the frog fauna than has accumulated in almost 80 years since Forrer made the first herpetological collections there.

Turtles

Kinosternon integrum[1]
Geoemyda pulcherrima
Pseudemys scripta

The fauna of coastal Jalisco is thought to include only two turtles in addition to *Kinosternon*. *Pseudemys scripta* is a large (carapace length up to at least 14 inches) aquatic species that lives in coastal swamps, lagoons, and larger streams. The only place where it might be expected on the Tres Marías is the lagoon on the northern side of María Magdalena. *Geoemyda pulcherrima* is a terrestrial species that frequents humid woods (Oliver, 1937, p. 8) and may yet be found on the Tres Marías.

Crocodile

Crocodylus acutus[1]

Lizards

Phyllodactylus lanei[1]
Anolis nebuloides
Anolis nebulosus[1]
Anolis schmidti
Basiliscus vittatus
Ctenosaura pectinata[1]
Iguana iguana
Sceloporus horridus
Sceloporus melanorhinus
Sceloporus pyrrhogaster
Sceloporus utiformis
Urosaurus bicarinatus
Eumeces parvulus
Scincella assata
Ameiva undulata
Cnemidophorus communis[1]
Cnemidophorus deppei
Heloderma horridum

The fewest additions to the herpetofauna of the Tres Marías are to be expected among the lizards. Four of 18 species inhabiting coastal Jalisco are known to live on the islands, and one additional northern form is present. Many of the 14 remaining species are conspicuous animals and, if present on the islands, surely would have been detected. Thus *Basiliscus*, *Sceloporus*, *Iguana*, *Ameiva*, and *Cnemidophorus deppei* would almost certainly have been collected if present. *Anolis nebuloides* and *A. schmidti* might be considered less obvious, but the presence of one *Anolis* in a region of relatively limited ecologic opportunity mitigates against the survival of other species. Similar reasoning may be applied to *Urosaurus bicarinatus*, represented on the islands by the similar species *U. ornatus*. The presence of the venomous *escorpión*, *Heloderma horridum*, would almost certainly be known to residents of the islands, but it was not reported to us. The only lizards unrecorded from the Tres Marías that might reasonably be expected there are skinks of the genera *Eumeces* and *Scincella*. Not only are these secretive forms likely to be overlooked, but, as small inhabitants of the forest floor, they occupy an ecologic niche not known to be filled on the islands.

Snakes

Leptotyphlops humilis
Leptotyphlops phenops
Boa constrictor[1]
Loxocemus bicolor
Coniophanes lateritius
Conophis vittatus
Dryadophis melanolomus[1]
Drymarchon corais[1]
Drymobius margaritiferus
Elaphe triaspis
Hypsiglena torquata
Imantodes gemmistratus[1]
Lampropeltis triangulum[1]
Leptodeira maculata
Leptodeira septentrionalis

[1] Species present on the Tres Marías Islands.

Leptodeira splendida
Leptophis diplotropis[1]
Manolepis putnami
Masticophis bilineatus
Masticophis lineatus[1]
Natrix valida
Oxybelis aeneus[1]
Pseudoficimia frontalis
Rhadinaea hesperia
Salvadora mexicana
Sibon nebulatus
Tantilla calamarina[1]
Trimorphodon paucimaculatus
Tropidodipsas occidentalis
Micrurus distans
Micrurus nigrocinctus
Agkistrodon bilineatus[1]
Crotalus basiliscus

Eleven species of snakes (excluding the sea snake) are known on the Tres Marías, compared with possibly 33 species in coastal Jalisco. Many species on the mainland list are secretive, burrowing, or nocturnal forms, rarely encountered even in relatively well-collected regions, so their eventual discovery on the islands would not be surprising. Active, diurnal species of the mainland, such as *Drymobius margaritiferus*, *Masticophis bilineatus*, and *Salvadora mexicana*, would probably have been found if present on the islands.

[1] Species present on the Tres Marías Islands.

Eight species (including, in addition to the three mentioned above, *Dryadophis melanolomus*, *Drymarchon corais*, *Masticophis lineatus*, *Leptophis diplotropis*, and *Oxybelis aeneus*) of the 33 on the list of mainland forms are active, diurnal forms and thus the snakes most likely to be collected. The known island fauna includes five active, diurnal forms out of a total of 11. The mainland ratio can scarcely be expected to be duplicated precisely on the islands, but it is probable that several of the secretive species are present but undetected on the islands.

Mention may be made here of the rattlesnake, which was recorded (as *Crotalus* sp.?) by Stejneger (1899, p. 71) from María Magdalena. The record was based on information given to E. W. Nelson and transmitted to Stejneger. On María Madre persons familiar with the local fauna, and able to recognize many of the snakes by vernacular names, insisted that no rattlesnakes were present on the islands. If truly present, the rattlesnake could scarcely escape detection in a region where scores or even hundreds of men work out of doors throughout the year. Nelson was almost certainly misled by his informant. There is a remote possibility that the snake is present on María Magdelana though not on María Madre, but this off chance scarcely allows the inclusion of *Crotalus* in the list of the insular fauna.

SUMMARY

THE TRES MARÍAS are a group of four islands located 59 to 70 miles off the Pacific coast of Mexico, opposite the State of Nayarit. The herpetofauna includes two species of anurans, one turtle, a crocodile, five lizards, and 11 snakes. A sea snake and at least two sea turtles occur in the waters about the islands. Little evolutionary divergence from mainland stocks has taken place, with only one endemic subspecies of snake and one endemic subspecies of lizard present. The status of an apparently endemic genus of snakes described from the islands cannot be evaluated, because the only known specimen has been lost.

Geographic relationships of the reptiles on the islands are predominantly southern; all species but one range to the south of the islands, and several reach Central and South America. With the exception of a single northern lizard, the reptiles and amphibians are thought to have reached the islands by way of a land connection now submerged. The exception is *Urosaurus ornatus*, which may have rafted to the islands. The population of this species on the Tres Marías is isolated more than 200 miles south of the main range of the species.

Review of the taxonomic status of several supposedly endemic subspecies of snakes reveals the need for synonymizing three names proposed for insular populations. These are listed below, with the current nomenclature on the left and the suggested names on the right:

Boa constrictor sigma (Smith)	= *Boa constrictor imperator* Daudin
Masticophis flagellum variolosus Smith	= *Masticophis lineatus* Bocourt
Drymarchon corais cleofae Brock	= *Drymarchon corais rubidus* Smith

In addition, a previous decision by Oliver to synonymize another snake (*Leptophis diplotropis forreri* Smith = *L. diplotropis* Günther) is followed.

This study is based largely on collections made on the Puritan-American Museum of Natural History Expedition to Western Mexico in the spring of 1957. Three species collected at that time are additions to the insular fauna, including the first reported anurans (*Syrrhophus modestus pallidus* and *Bufo mazatlanensis*) and a snake (*Tantilla calamarina*).

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