GEOGRAPHIC VARIATION AND DISTRIBUTION OF THE GENUS TOMODACTYLUS IN MEXICO

A Thesis

By

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INTRODUCTION

Mexico is of increasing importance and interest to herpetologists; recent improvements in road conditions have made available many regions that were once inaccessible. The opening of these little known regions has enabled investigators in many biological fields to close distributional gaps and to record new ecological data on many groups of animals. Many new species of animals have been described and faunal relationships have become clearer.

Mexico was relatively unexplored by herpetologists prior to the turn of the century. Peters (1869) was one of the earliest workers. He was soon followed by such men as Gunther (1900), Gadow (1910), and Ruthven, all of whom pioneered in herpetological investigations of Mexico and stimulated the interests of later herpetologists.

Many recent biological investigations in Mexico have been conducted by or supported by universities, colleges, and museums of the United States. The vegetation zones were described by Leopold (1950). The biotic communities were described by Goldman and Moore (1945) and by E. A. Goldman (1951). The herpetogeny of Mexico was studied by Smith (1949). In recent years there has been an ever increasing number of publications on herpetological material

from Mexico which is an indication of the broadened interest in that area.

A comprehensive knowledge of some of the lesser known forms of amphibians and reptiles of Mexico should ultimately clarify some of the problems concerning their distribution and relationships. The status of Tomodactylus as a genus and its relationship to other genera of the family Leptodactylidae have been uncertain for a number of years. Both Parker (1927) and Firschein (1954) questioned the validity of Tomodactylus as a genus; however, it has generally been accepted as valid by herpetologists who are familiar with the group. Recent workers, such as Taylor (1940) (1943), Duellman (1954), and Davis and Dixon (1955), have expanded the number of known species in the genus from two to seven.

There has been available little life history information for this genus, due in all probability to the secretive habits of the animals. Martin del Campo (1940) published a note on the incubation and hatching of the eggs of Tomodactylus nitidus. The breeding habits of T. angustidigitorum were briefly reported on by Schmidt and Shannon (1947) and other workers have published short notes on their habitat preferences.

As indicated above, many facts were lacking regarding the distribution and taxonomic status of Tomodactylus.

Consequently, this study has been an attempt to gather information on that genus with the hope that a clearer picture could be gained regarding speciation in the group. The problem regarding the relationship of Tomodactylus to other closely related leptodactylids is beyond the scope of this study.

The study has two principal objectives: First, to determine the geographic variation of the known species of Tomodactylus. The various subspecies and species are discussed and available life history notes are reported. Second, to determine the geographic distribution of the genus and its component species.

Much of the material available for this study was borrowed from various universities and museums, but freshly preserved material was obtained in the Mexican states of Mexico, Morelos, and Guerrero from 1949 through 1954 by students of the Department of Wildlife Management, A. & M. College of Texas, under the direction of Dr. W. B. Davis and Dr. K. L. Dixon. In addition I spent six weeks in Mexico during June and July, 1954, and again in 1956 for the purpose of collecting specimens, recording ecological data, and closing existing gaps in the recorded distribution of the genus.

Geographic Distribution of the Genus

Beginning at the north and proceeding southeastward, the known range includes all, or parts of, the states of Sinaloa, Nayarit, Jalisco, Colima, Michoacan, Guanajato, Mexico, Distrito Federal, Guerrero, Morelos, Puebla, Veracruz, and Oaxaca (see Map 1). It includes many physiographic provinces (discussed below under the heading Environmental Considerations). Elevations within this range vary from sea level along the Pacific coast to 8,800 feet in the Ajusco Mountains of south-central Mexico.

Methods and Treatments

The study is based primarily on specimens in the Texas Cooperative Wildlife Collection at the Texas A. & M. College. Additionally, specimens were borrowed from universities, museums, and private collections. Abbreviations of these collections are as follows: AMNH, American Museum of Natural History; BMNH, British Museum (Natural History); CNHM, Chicago Natural History Museum; FAS, Fredrick A. Shannon; RWA, Ralph W. Axtell; TCWC, Texas Cooperative Wildlife Collection; UIMNH, University of Illinois Museum of Natural History; UKMNH, University of Kansas Museum of Natural History; UMMZ, University of Michigan Museum of Zoology; USNM, United States National Museum.

Notes on color, breeding habit, and habitat were

recorded by me in the field. The following measurements, in millimeters, were made in the laboratory with a vernier caliper to the nearest 0.1 millimeter:

Snout-vent length: Length from tip of snout to anus.

Foot length: Length from tip of longest toe to proximal edge of inner metatarsal tubercle. The foot is usually measured from the tip of the longest toe to the heel, but specimens are often so poorly preserved that this measurement is not constant.

Tibial length: Length from distal end to the proximal end of tibia.

Head length: Length from tip of snout to end of frontal-parietal bone.

Head width: Width across head at posterior angle of jaw.

Eye width: Greatest diameter of eye, measured from anterior to posterior corners.

Tympanic width: Measured from lower rim to upper rim of tympanum. This measurement is not always vertical but may be diagonal, depending upon the shape of the tympanum.

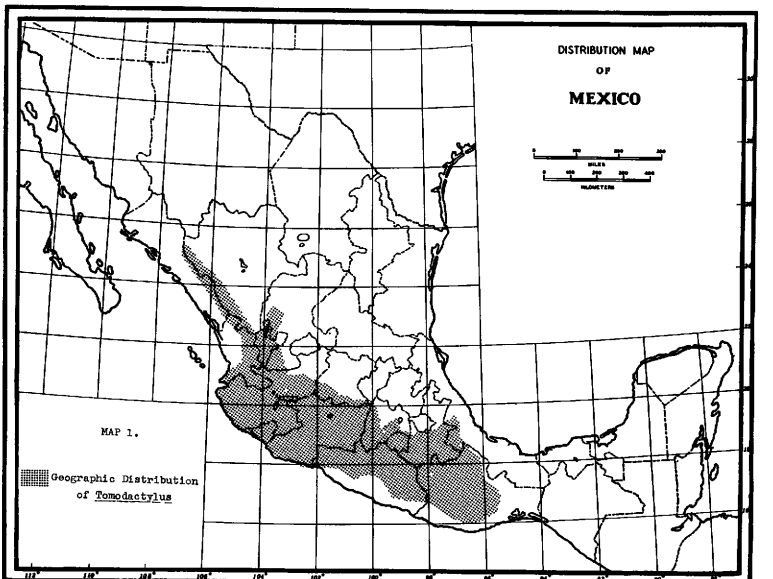
Interorbital width: Distance between orbits. Measured from outer edges of paired frontal-parietal bones.

Internarial width: Distance between medial borders of nostrils.

Length of inguinal gland: Length from anterior to posterior

outlines of inguinal gland.

In all, 848 specimens of Tomodactylus were measured for this study. Six measurements, snout-vent length, foot length, tibial length, eye width, tympanic width, and internarial width, were used in the stastical analysis of each species. Standard formulae were used to determine the variance, mean, standard error, standard deviation, and significance. The other measurements listed above were found to be too variable for statistical treatment. However, these measurements are discussed in the final analysis of the species. The most wide ranging species was selected and treated statistically to ascertain the extent of variation. Graphs and tables were prepared to simplify and clarify the results. An analysis of interspecific differences then follows. The results were again illustrated by tables to emphasize the similarities and differences of the various species. A general discussion follows the subspecies and species accounts in which taxonomic relationships and environmental considerations are elaborated upon.


DISTRIBUTION MAP
OF
MEXICO
MILES
KILOMETERS
MAP 1.
Geographic Distribution
of Tomodactylus

GAZETTEER

Specimens are available from 141 collecting localities throughout the range of Tomodactylus. Because of the large number of localities, the following list of towns is used as reference points for sites at which Tomodactylus has been taken.

In the list below, the states are arranged generally from north to south; the towns within each state, alphabetically. The name of each town is followed by (1) co-ordinates to the nearest minute of west longitude and north latitude; (2) an approximate elevation determined from maps or by aneroid barometer; (3) a location number, which corresponds to the position of the town on the accompanying map (Map 2); (4) a statement of the vegetation type that occurs there.

SINALOA

Concordia. 106°04';23°17'; 99 ft.; Location 1. Tropical Deciduous Forest. A small village in the foothills of the Sierra Madre Occidental.

NAYARIT

Ahuacatlan. 104°25';21°03'; 3,300 ft.; Location 5. Scrub oak in the Pine-oak Forest.

El Ocotillo. 104°38';21°10'; 2,300 ft.; Location 4. Tropical Deciduous Forest. A small village in a

deep valley with the surrounding vegetation somewhat thorny.

Las Chivas. 105°01';21°36'; 300 ft.; Location 2. Thorn Forest. An Indian village on the southern edge of the National Marshlands of Mexico.

Tepic. 104°54';21°30'; 3,000 ft.; Location 3. Pine-oak Forest. Originally a pine-oak association but extensive agriculture has reduced the vegetation to a disclimax of thorny shrubs and short grasses.

JALISCO

Amatitlan. 103°17';20°49'; 4,000 ft.; Location 7. Pine-oak Forest. An extensive agricultural center for the production of maguey.

Autlan. 104°18';19°50'; 3,000 ft.; Location 10. Pine-oak Forest. A large railroad shipping center in southwestern Jalisco.

Guadalajara. 103°20';20°40'; 5,100 ft.; Location 8. Pine-oak Forest. The state capitol and pottery center of Jalisco.

Magdalena. 103°57';20°54'; 4,500 ft.; Location 6. Pine-oak Forest. A small railroad station in northwestern Jalisco.

Santa Cruz de las Flores. 103°28';20°30'; 5,200 ft.; Location 9. Pine-oak Forest. A small village

in the Valle de Cocula.

GUANAJUATO (no specific locality)

COLIMA

Colima. 103°43';19°15'; 1,500 ft.; Location 80. Tropical Deciduous Forest. The capitol of the state of Colima.

Hacienda Paso del Rio. 104°20';19°03'; 50 ft. Location 12. Thorn Forest. A small railroad station on the Rio de Armeria.

Manzanillo. 103°56';18°56'; 15 ft. Location 11. Thorn Forest. Main seaport in the state of Colima.

Tecolapa. 103°49';19°02'; 450 ft.; Location 81. Thorn Forest. A small village in southern Colima.

MICHOACÁN

Angahuan. 102°10';19°35'; 7,000 ft.; Location 19. Pine-oak Forest. A small town on the north slope of Cerro de Tancitaro.

Apatzingan. 102°21';19°05'; 1,100 ft.; Location 79. Tropical Deciduous Forest. A small village in the lower Balsas Valley.

Apo. 102°20';19°24'; 6,800 ft.; Location 22. Pine-oak Forest. A small village on the west slope of Cerro de Tancitaro.

Carapan. 102°02';19°52'; 6,700 ft.; Location 17.

Pine-oak Forest. The mountains just south of Carapan contain one of the few virgin pine-oak forests still in existence in Mexico.

Charapendo. 102°11';19°13'; 3,000 ft.; Location 78. Tropical Deciduous Forest. A small town in the lower Balsas Valley.

Coalcoman. 103°10';18°46'; 3,500 ft.; Location 14. Tropical Deciduous Forest. A railroad center in western Michoacan.

Copullo. 100°55';19°35'; 6,000 ft.; Location 31. Tropical Deciduous Forest. A small village on the road from Morelia to Huetamo.

Corupu. 102°12';19°37'; 6,800 ft.; Location 20. Pine-oak Forest. A small village on the northwestern slops of Cerro de Tancitaro.

Jiquilpan. 102°42';19°59'; 5,500 ft.; Location 15. Pine-oak Forest. A large village in a broad fertile plain which is farmed extensively for the production of sugar cane and wheat.

Morelia. 101°07';19°42'; 6,200 ft.; Location 30. Pine-oak Forest. The state capitol of Michoacan. The surrounding valleys are used primarily for the growing of garden and truck crops.

Paricutin. 102°13';19°25'; 6,500 ft.; Location 21.

Pine-oak Forest. The village of Paricutin lies only a few miles to the north of Volcan Paricutin; the most recent active volcano in Mexico.

Patzcuaro. 101°31';19°31'; 6,900 ft.; Location 28. Pine-oak Forest. A large town surrounded by low hills on the southern edge of Lago Patzcuaro. Large areas of lava deposits lie to the south.

Pomaro. 103°13';18°20'; 3,200 ft.; Location 13. Thorn Forest. A small village near the Rio Cachan in western Michoacan.

Quiroga. 101°30';19°42'; 6,800 ft.; Location 27. Pine-oak Forest. A small town near Lago Patzcuaro and the type locality for T. angustidigitorum.

San Juan Parangaricutiro. 102°14';19°30'; 6,500 ft.; Location 24. Pine-oak Forest. A small village on the southeastern slope of Cerro de Tancitaro.

Tancitaro. 102°17';19°22'; 6,800 ft.; Location 23. Pine-oak Forest. A small town on the southern slope of a mountain of the same name.

Tuxpan. 100°28';19°34'; 6,100 ft.; Location 77. Pine-oak Forest. A small resort village 100 miles west of Mexico City.

Tzinzuntzan. 101°30';19°37'; 6,800 ft.; Location 29. Pine-oak Forest. The ancient capitol of the

Pagan Tarascan Empire.

Uruapan. 101°57';19°25'; 5,200 ft.; Location 25. Pine-oak Forest. A large town in a narrow valley which is farmed extensively for the production of bananas, coffee, and maguey.

Volcan de Jorullo. 101°42';18°59'; 4,200 ft.; Location 26. Tropical Deciduous Forest. A volcanic cone at the base of the southern edge of the Mexican Plateau. The summit vegetation is predominantly pine-oak.

Zacapu. 101°45';19°49'; 6,800 ft.; Location 18. Pine-oak Forest. Zacapu is a large town situated in the center of a rich agricultural region. Corn and maguey are the important cultivated crops.

Zamora. 102°18';19°59'; 5,200 ft.; Location 16. Pine-oak Forest. Zamora lies in the lap of a large fertile valley. The surrounding hillsides are predominantly oak.

MÉXICO

Ixtapan de la Sal. 99°34';18°50'; 5,200 ft.; Location 34. Pine-oak Forest. A small village on the southern slope of Volcan Zinantecatl (Volcan de Toluca).

San Martin. 98°50';19°42'; 8,000 ft.; Location 35.

Pine-oak Forest. This area is farmed extensively for the production of maguey.

Tenancingo. 99°33';18°55'; 6,700 ft.; Location 33. Pine-oak Forest. This region is predominantly pine with open stands of oaks.

DISTRITO FEDERAL

San Pedro. 99°10';19°10'; 7,800 ft.; Location 38. Pine-oak Forest. A small town on the northeastern slope of Cerro de Ajusco.

Tlalpan. 99°17';19°10'; 7,600 ft.; Location 37. Pine-oak Forest. A suburb of Mexico City at the southern end of the Valle de Mexico.

Villa Alvaro Obregon. 99°06';19°25'; 7,800 ft.; Location 36. Pine-oak Forest. A large suburb of Mexico City.

MORELOS

Alpuyeca. 99°15';18°44'; 3,500 ft.; Location 50. Arid Tropical Scrub. A small town surrounded by rolling hills and irrigated valleys. The major crops are rice, corn, and bananas.

Axochiapan. 98°45';18°30'; 3,500 ft.; Location 52. Arid Tropical Scrub. A small village in the center of an open plain where the main crop is corn.

Cuautla. 98°58';18°48'; 4,200 ft.; Location 44.

Tropical Deciduous Forest. The major vegetation has been reduced to short grasses, scattered oaks, and hardwoods.

Cuernavaca. 99°14';18°55'; 5,200 ft.; Location 42. Tropical Deciduous Forest. The state capitol of Morelos and now under a pronounced disclimax towards arid tropical scrub.

El Rodeo. 99°20';18°43'; 3,500 ft.; Location 49. Arid Tropical Scrub. A small lake about 6 miles west of Alpuyeca.

Huitzilac. 99°15';19°01'; 8,200 ft.; Location 39. Pine-oak Forest. A farming community in an open pine-oak association.

Huyaptlan. 99°25';18°36'; 3,100 ft.; Location 54. Arid Tropical Scrub. A small community surrounded by shallow rocky soils and low rolling hills.

Jonacatepec. 98°49';18°40'; 4,000 ft.; Location 51. Arid Tropical Scrub. The main agricultural crop in the area is corn.

Progreso. 99°10';18°55'; 5,000 ft.; Location 43. Tropical Deciduous Forest. Rice is the main crop grown in this area.

Puente de Ixtla. 99°19';18°37'; 2,800 ft.; Location 53. Arid Tropical Scrub. This area is composed of

low rolling hills and thin rocky soils.

Tepotztlan. 99°06';18°59'; 5,700 ft.; Location 41. Tropical Deciduous Forest. A heavily farmed area just below the pine-oak association.

Tres Marias. [= Tres Cumbres]. 99°13';19°03'; 7,200 ft.; Location 40. Pine-oak Forest. A small village a few miles north of Cuernavaca.

Yautepec. 99°04';18°53'; 3,900 ft.; Location 45. Tropical Deciduous Forest. The main crops of this area are rice and sugar cane.

PUEBLA

Acatlan. 98°03';18°12'; 4,100 ft.; Location 71. Tropical Deciduous Forest. This area has a distinct tendency towards the arid tropical scrub association.

Cholulu. 98°18';18°04'; 7,000 ft.; Location 46. Pine-oak Forest. A large town about 10 miles west of Puebla, state capitol.

Matamoros de Izucar. 98°27';18°36'; 4,600 ft.; Location 69. Arid Tropical Scrub. This area is the type locality for T. nitidus.

Tehuacan. 97°22';18°27'; 5,400 ft.; Location 70. Arid Tropical Scrub. This locality is in a large flat valley with a solid limestone floor.

VERACRUZ

Agultzingo. 97°19';18°42'; 7,000 ft.; Location 48. Pine-oak Forest. A small town at the lower edge of the pine-oak association.

El Chico. 96°50';19°28'; 3,500 ft.; Location 47. Tropical Evergreen Forest. A small town on the western slope of the Sierra Madre Oriental.

GUERRERO

Acahuizotla. 99°27';17°22'; 2,800 ft.; Location 66. Tropical Deciduous Forest. A small village at the upper level of the mixed forest association.

Agua del Obispo. 99°28';17°19'; 3,300 ft.; Location 67. Pine-oak Forest. Open pine forest near the lower level of Pine-oak Forest association.

Almolonga. 99°18';17°38'; 5,600 ft.; Location 63. Pine-oak Forest. A scrub oak community in the pine-oak forest association.

Chilpancingo. 99°30';17°33'; 4,600 ft.; Location 60. Arid Tropical Deciduous Forest. The state capitol of Guerrero and agricultural center of the region.

Colotlipa. 99°09';17°25'; 2,700 ft.; Location 68. Tropical Deciduous Forest. This area has a distinct tendency towards the thorn forest association.

El Limon. 101°41';18°05'; 2,600 ft.; Location 32.

Arid Tropical Deciduous Forest. A small village on the western slope of the Sierra Madre del Sur.

El Naranjo. 99°32';18°24'; 4,000 ft.; Location 56. Arid Tropical Scrub. A railroad station in northeastern Guerrero.

Iguala. 99°32';18°20'; 2,400 ft.; Location 57. Arid Tropical Scrub. An area of steep hills and broad valleys. The main crops are rice and crop.

Mazatlán. 99°27';17°27'; 4,000 ft.; Location 64. Tropical Deciduous Forest. A small village approximately 24 miles southwest of Chilpancingo.

Mexcala. 99°37';17°56'; 1,350 ft.; Locality 59. Arid Tropical Scrub. A small village on the south bank of the Rio Balsas.

Omiltemi. 99°39';17°33'; 7,800 ft.; Location 61. Pine-oak Forest. A logging village just below a cloud forest association.

Palo Blanco. 99°29';17°26'; 3,800 ft.; Location 65. Tropical Deciduous Forest. A small village just below the pine-oak forest association.

Taxco. 99°36';18°33'; 5,500 ft.; Location 55. Pine-oak Forest. Taxco is the famous silver center of Mexico.

Tixtla. 99°24';17°34'; 4,400 ft.; Location 62.

Tropical Deciduous Forest. Tixtla was once the capitol of Guerrero but is now reduced to a small town.

Tonalapan. 99°33';18°06'; 2,700 ft.; Location 58. Arid Tropical Scrub. A very small village about 10 miles east of the Rio Balsas.

OAXACA

Cuicutlán. 96°57';17°48'; 1,800 ft.; Location 72. Arid Tropical Scrub. The town is situated in the middle of a narrow valley surrounded by steep limestone and sandstone hills.

El Coyul. 95°58';16°35'; 2,800 ft.; Location 76. Tropical Deciduous Forest. The southernmost collecting site of the genus Tomodactylus.

Nochixtlán. 97°13';17°27; 6,900 ft.; Location 74. Pine-oak Forest. A town of considerable size located in the center of the Sierra Madre del Sur.

Oaxaca de Juarez. 96°44';17°04'; 5,100 ft.; Location 75. Pine-oak Forest. The city lies in a valley of the same name. Due to extensive agriculture, the vegetation is in a disclimax of arid tropical scrub.

Yanhuitlán. 97°23';17°33'; 7,000 ft.; Location 73. Pine-oak Forest. This area is in a state of extensive erosion caused by clearing the surrounding forests.

ENVIRONMENTAL CONSIDERATIONS

Physiography. The geographic range of Tomodactylus includes many of the outstanding topographic features of Mexico. According to Ordonez (1936), the physiography of Mexico comprises twelve provinces and nine sub-provinces. Thayer (1916) states that Mexico is divided into seven natural provinces on the basis of a common feature that was in existence in the tertiary era. Hill (1908) suggested the name "Cordilleran Peneplain" for this feature. Generally, Ordonez follows Thayer's descriptions of the physiographic provinces but separates some of the provinces into subdivisions. Additionally, Ordonez described several provinces that were not recognized by Thayer. I prefer to follow the features presented by Ordonez because of the more detailed account of the physiographic regions and the addition of new provinces that aid in clarifying the distribution of the genus Tomodactylus.

Seven physiographic provinces (Ordonez, 1936:1279) are found within the range of the genus Tomodactylus, as follows:

Coastal Strip of Sinaloa and Nayarit Province: This province is a continuation of the Sonora Desert for some 500 miles toward the south. The province is bordered on the east by the Sierra Madre Occidental and on the west by the

Pacific Ocean. The region receives more rainfall, maintains a higher humidity and subsequently has more vegetation than that of the Sonoran Desert. Isolated mountain ranges are common in the southern portion of the province, which includes parts of the states of Nayarit and Jalisco. Prior to the last uplift and present erosion, these isolated sierras were probably part of the Sierra Madre Occidental that extended to the coast. The final development of the coastal strip was due to local volcanic flows which rejuvenated much of the older degraded topography and introduced many changes (Ordonez; op.cit.:1284). This region is presently under intensive agricultural use and is mined for silver and lead.

Western Sierra Madre Province: This province comprises a vast mountain range extending from the Sonoran Desert in the northwest to the Balsas Basin in the southwest. Its width varies but reaches 200 miles in some places. The average elevation is about 7,000 feet; a few of the summits exceed 10,000 feet. The province has no direct physiographic continuation in the United States because it is cut off by the Sonoran Desert and the north-central plateau provinces which form the Mexican Highlands (Ordonez, op. cit.:1285).

It has been supposed that the physiographic aspects of the Western Sierra Madre Province were formed by a large and almost uniform uplift. Later uplifts shifted portions of

the range but, as a whole, the individual sierras connect with one another. Recent basaltic flows and minor eruptions have not changed the main features of the province. Erosion appears to be young and the canyons are still deep and narrow. The western side of the province contains a large number of rivers that originate near the eastern edge of the mountains and flow westward to the Pacific Ocean. The southeastern edge of the province merges gradually into the central plateau of Mexico (Ordonez, op. cit.:1286). Rainfall within the province ranges from 25 to 30 inches. The climate ranges from hot in the lower valleys to temperate at the summits (Ordonez, op. cit.:1287).

The province as a whole embraces several vegetation types which are discussed below under the heading Vegetation Zones. Cattle, mining, timber, and farming are the chief sources of income for this province. In recent years the absence of supervision and guidance in the cutting of timber and in agricultural practices have brought about a disclimax of vegetation in many of the populated sections of the province.

Eastern Sierra Madre Province: The province extends from the Big Bend region of Western Texas to the Isthmus of Tehuantepec in southern Mexico. This range of mountains faces the Gulf of Mexico and is quite narrow throughout its

length. The sierras in the extreme northern parts of the province are separated to some extent but merge gradually into one massive range of mountains to the south. The geology of the region is primarily limestone of Mesozoic age with some shales and sandstones (Ordonez, op. cit.:1289).

Erosion of the thick limestone beds is relatively slow which leaves the impression that the erosive cycle is young, but more advanced erosion may be seen in mountains made of volcanic or other sedimentary deposits. The average elevation of the region is 7,000 feet with summits often reaching 10,000 feet. The highest summit in Mexico is found in this province. Pico de Orizaba in the southern portion of the region reaches an elevation of 18,400 feet above sea level (Ordonez op. cit.:1288).

The rainfall of this region exceeds that of the Western Sierra Madre Province. The rainy season starts two weeks to a month earlier in the eastern sierras, usually in May, and lasts until September. The central portion of the province, including some of the steep slopes of the mountains, is under intensive agriculture. The valleys are farmed for the production of corn, papaya, bananas, and citrus fruits. The mining of copper, gold, silver, and lead ore deposits is important.

Central Plateau Province, South-central Sub-province:

The south-central sub-province is separated from the north-central sub-province by its higher elevations, broader and more extensive valleys and volcanic orgin. Thayer (1916:84) calls this area the "volcanic province" because of the extent of volcanic action in the region. Ordonez (1936:1291) indicates that the present elevation of the region was due to the large quantities of volcanic materials that poured out of craters and fissures of massive volcanos. An indication of the vast lava flows is still evidenced by the large volcanos bordering the southern edge of the province. The largest of these is Popocatepetl, which rises to 17,830 feet, followed by Ixtaccihuatl 16,900 feet, Toluca 13,000 feet, and Colima 12,664 feet.

The present topography is one of large flat fertile valleys separated by short mountain barriers. Mining districts are dotted throughout the province. Silver-lead, lead, and copper-gold ores are the primary sources of wealth in the mining areas. The large valleys are cultivated for the production of corn, maguey, and garden vegetables. The average elevation is approximately 8,000 feet and the average temperature is about 78° F. The rainy season is from May to September; the rest of the year is very dry.

Balsas Basin Province: According to Thayer, (1916:91)

the Rio Balsas forms the northern edge of the Sierra del Sur Province. This area is divided by Ordonez, (1936:1294) into three provinces; the Balsas Basin, Southern Sierra Madre, and Valley of Oaxaca. Ordonez (op. cit.:1294) states the Rio Balsas has played an important part in forming what is now considered the Balsas Basin. The Basin is bordered on the north by the volcanic escarpment of the south-central plateau, on the south by the Sierra Madre del Sur and on the east by the Eastern Sierra Madre. The Rio Balsas receives the waters of the three mountain ranges surrounding it and carries the water to the Pacific Ocean.

The topography is a rough broken mountainous terrain with numerous short rivers emptying into the Rio Balsas. The rainy season is short, but rains are often intense. The interior of the basin is hot and dry during most of the year. The prevailing winds seem to vary from time to time, lose most of the moisture in the mountains, and leave much of the province dry.

The valleys of this region are cultivated for the production of corn, as in most areas of central Mexico. Large quantities of various fruits are also produced near the coast where rain is more abundant.

Southern Sierra Madre Province: The mountains of this province parallel the Pacific Coast in a northwest-southeast

direction. Generally, they rise close to the ocean and leave no room for the development of a coastal plain. Elevations range from sea level to over 8,000 feet but average about 6,500 feet. Rainfall is heavy from May to October, and the southwestern and southern slopes of the sierras maintain a dense growth of vegetation. The northern and northeastern slopes have much less rainfall, higher temperatures, and subsequently less vegetation. There are many areas of this province yet to be explored. The roads in this region are poor, probably because of a sparse human population and the imposing mountain barriers.

The valleys are farmed but the primary wealth is in the form of mineral deposits. At the mouth of the Rio Balsas in the northwestern end of the province lies the largest deposit of iron ore in Mexico. It has been estimated that fifteen million tons of iron ore are exposed at the surface (Ordonez, op. cit.:1296).

Valley of Oaxaca Province: The Valley of Oaxaca lies at the junction of the Sierra Madre del Sur and the Sierra Madre Oriental. The valley is approximately 60 miles long and 10 to 15 miles wide. The average elevation is 5,000 feet and rainfall is heavy from June to September. The climate is mild due to the location, elevation and latitude of the valley.

Mining and agriculture are the principal occupations of the inhabitants in this region. Gold and silver ores are abundant in several areas. Corn is the main agricultural crop. The geological aspects of the valley are important because the province contains features of all the adjoining provinces. According to Ordonez (op.cit.:1306) the valley was once the seat of the ancient Mixtecan and Zapotecan civilizations.

Vegetational Zones

The most recent and reliable information on the vegetation of Mexico was compiled by A. S. Leopold (1950), who attempted to map the original major vegetative types as they existed before they were influenced by man. He considers the southern regions of the Mexican Plateau as a Pine-oak Forest, but, due to the inroads of man, the major portions are completely denuded of any type of forest. This is true of other regions in Mexico where man has introduced agriculture.

My field observations agree with those of Leopold where relic areas were observed, but in other instances the original vegetation could only be assumed. For the purpose of this study I have followed Leopold. He (op. cit.:507) separates the vegetation of Mexico into two series, temperate and tropical, with twelve types. Tomodactylus occurs in one of the temperate and four of the tropical types, as follows:

Temperate, Pine-oak Forest; Tropical, Thorn Forest, Tropical Deciduous Forest, Arid Tropical Scrub, and Tropical Evergreen Forest. Following is an account of each of the vegetation zones occupied by the genus Tomodactylus.

Pine-oak Forest. The pine-oak zone is the largest vegetation type in Mexico. Leopold (op. cit.:510-511) lists four distinct communities in this zone, as follows: Pine Forest, Pine-oak Woodland, Pinon-juniper Woodland, and Oak Scrub. The Pinon-juniper Woodland does not occur within the range of Tomodactylus. The pine forest community is variable in elevation and in its dominant vegetation. The elevation and presence or absence of certain species of pines are controlled by prevailing winds, slope exposure, moisture, and temperature. This community is most commonly encountered between elevations of 7,000 and 8,000 feet. The most common pine according to Leopold is Pinus montezumae. Under certain climatic and physiographic conditions other pines such as P. herrerai, P. pseudostrobus, and P. ayacahuite are dominant.

The pine-oak woodland community occurs frequently at elevations of 5,000 to 7,000 feet between the pine forest and the oak scrub communities. Open scattered stands may be dominated by oak in some areas and by pine in others. The common pine in the southern district of this community is Pinus montezumae. Various species of oaks, such as Quercus

acutifolia, Q. langeria, Q. candicans, Q. mexicana, and Q. greggii, are scattered throughout the community.

The oak scrub community is commonly found along the lower elevations between the pine-oak community and the semi-arid foothills at elevations between 3,000 and 5,000 feet. The most common oaks are Q. glaucophylla and Q. glaucoides.

Tropical Deciduous Forest. The portions of the range of Tomodactylus within the tropical deciduous forest are along the western coastal plain, in the semi-humid foothills of the Balsas Basin, and in south-central Mexico. Among the principal tree genera of this forest in southwestern Puebla listed by Leopold (op. cit.:515) are Hauya, Coccoloba, Pseudosmodingium, Bursera, Conzattia, Fouquieria, and Ruprechtia along the hillsides; Pithecolobium and Prosopis in the alluvial bottoms; and Ficus, Salix, and Taxodium along the stream banks.

Arid Tropical Scrub. The arid tropical scrub zone is found in the western and south-central basins of southern Mexico. The Balsas Basin, southern Puebla, and northern Oaxaca are included within this zone. Leopold (op. cit.: 516) lists the following genera as being dominant in the Canon de Zopilote, Guerrero: Cephalocereus, Acacia, Mimosa, and Caesalpinia; along the more humid uplands, Bauhinia, Zizyphus, and Desmanthus. In southern Puebla and northern

Oaxaca, Cereus, Pilocereus, Fouquieria, Prosopis, and Opuntia are the dominant plants on the hillsides while Taxodium and Ficus are more prevalent along the streams.

Thorn Forest. Along the west coast from Sinaloa south to central Guerrero, a portion of the geographic range of Tomodactylus occurs within the thorn forest zone. In northern Sinaloa the dominant plant genera are Acacia, Cassia, Coutarea, Ceiba, and Prosopis. The dominant vegetation along the coastal areas of Guerrero consists of Acacia, Mimosa, Caesalpinia, and Cassia. The tropical regions along the western coastline of Mexico are quite arid in many sectors. This is due not only to the absence of rain but also to the saline conditions found along the coast.

Tropical Evergreen Forest. The tropical evergreen forest zone does not occur within the range of Tomodactylus. In west central Veracruz much of the tropical evergreen forest has been removed for agricultural purposes and a secondary growth of arid tropical scrub has invaded these regions. One species of Tomodactylus has been collected there.

SYNOPSIS OF THE GENUS

The genus Tomodactylus is a member of the family Leptodactylidae and like that family it contains many complex features. The earliest generic and specific name for this toad appears to be Liuperus (sic) nitidus described by Peters in 1869. In 1900 Gunther described the genus Tomodactylus and subsequently one species which he called T. amulae. He also separated Tomodactylus from other related genera, such as Paludicola and Leiuperus, on the basis of the presence of digital disks. He further ascribed to the genus the following characteristics: (1) no vomerine teeth, (2) tongue indistinctly notched behind or entire, (3) tympanum distinct, (4) outer metatarsals united, (5) fingers and toes free with small truncate dilations, (6) sternum with a boney style, (7) presence of a lumbar (inguinal) gland.

Parker (1927) questioned the validity of Tomodactylus as a genus and, while revising the genus Paludicola under which the generic name Leiuperus had been submerged, he discovered that a specimen of Leiuperus nitidus in the British Museum of Natural History was scarcely distinguishable from the type specimen of T. amulae described by Gunther. Nevertheless he referred the specimen of nitidus to the genus Tomodactylus until the position of the genus could be

satisfactorily determined. Firschein (1954) also questioned the validity of Tomodactylus as a genus. In recent years the inguinal gland has been relied on heavily as a criterion for the identification of Tomodactylus, but Firschein (op. cit.:50) questioned this criterion as an index character at the generic level because of the presence of an inguinal gland in the genus Syrrhophus. He used a combination of characters in delimiting Syrrhophus from Tomodactylus and other closely related genera. I have examined approximately 1,000 specimens of Tomodactylus and I find that many of the characters used by Firschein do not separate the two genera. I have found, however, additional characters that do separate them readily, as follows: (1) presence or absence of granulation on venter, (2) relative length of hind limbs, (3) relative width of head to body, (4) distinctiveness of inguinal gland.

With the exception of one species, all Tomodactylus share the following characteristics: (1) venter wholly or partly granular, (2) hind limbs relatively short, (3) head narrower than body, (4) inguinal or lumbar gland distinct. There is a misleading factor involved in the subjectivity of a distinct or indistinct inguinal gland that should be clarified. If specimens of Tomodactylus are properly preserved, the inguinal gland is distinct. Occasionally,

however, poor preservation distends the body and eradicates the outline of the gland. In no case has subsequent study of laboratory material failed to confirm my identification of Tomodactylus in the field on the basis of the inguinal gland.

T. macrotympanum Taylor, does not agree with any of the above characters of Tomodactylus but, instead, with those found in Syrrhophus, which are as follows: (1) venter smooth, the sides often granular, (2) hind limbs relatively long, (3) indistinct inguinal gland, (4) head wider than body. On the basis of the above characters I propose the transfer of macrotympanum to the genus Syrrhophus.

THE TOMODACTYLUS NITIDUS-PETERSI COMPLEX

At present Tomodactylus nitidus and T. petersi are recognized as distinct species. Until recently no one has been able to procure large enough samples of either species to warrant a statistical study of their relationships. I have examined some 330 adult T. nitidus and 87 adult T. petersi and analyzed them statistically. I find that there is a much closer relationship between them than was formerly believed. Tomodactylus nitidus was described by Peters in 1869 and is by far the widest-ranging form of the genus. Duellman (1954) described T. petersi, a form second to T. nitidus in extent of range.

Duellman (1954:7) based his species concept on several characters that appeared to separate T. petersi from closely related forms. These are (1) longer legs than in other species; (2) greater expansion of digits; (3) indistinct inguinal gland; (4) few dorsal pustulations and smooth venter; (5) darker color of spot on face of femur and in groin. I find, however, that none of these holds true. He described petersi on the basis of 11 specimens collected by J. A. Peters; he had available only a small series of T. nitidus for comparison. Duellman worked entirely with preserved material, a circumstance which may explain the

differences found in the condition of the skin and inguinal gland. These characters often become indistinct or disappear in preserving fluid. The small series with which he had to work explains the differences in leg length, color of femur and groin, and expansion of digits that I find in analysis of a larger series (87 specimens).

There appears to be a continuous color gradient in the dorsal and ventral patterns between petersi and nitidus. Contrary to Gloger's rule for warm-blooded vertebrates (Mayr, 1942:90) there seems to be an increase in the melanins towards the northern end of the range of each species. The climatic conditions at the northern limit of petersi are arid, even in the coastal region. This condition also prevails in the northern limits of the range of nitidus, primarily, in the lower Balsas Basin, but brownish pigments are more frequent in specimens from there and in the mountains of southern Oaxaca. Specimens of petersi from the foothills of eastern Sinaloa at an elevation of 4,800 feet are melanistic.

In contrast to the dorsal coloration, the immaculate spot of color that occurs on the anterior face of the femur and in the groin shows a parallelism to Gloger's rule. In the arid regions of the Balsas Basin and southern Oaxaca, nitidus has a light yellow or yellowish white spot on the

femur and groin. In the humid foothills toward the mouth of the Rio Balsas petersi have yellowish orange or orange spots, but as one continues northward into a more arid habitat, the color becomes lighter.

Specimens of nitidus from localities progressively closer to the range of petersi show an increase in the size of the tympanum and in the width of the tips of the two outer fingers. At the same time, petersi shows a decrease in the size of these structures as one progresses from north to south. Nevertheless, a sharp distinction in tympanic width between the two is evident when they are compared in a total analysis. The length of the leg in the two species is approximately the same and absolute sizes and proportions of the foot and tibia are almost identical. T. nitidus is slightly larger in all respects with the exception of the tympanic width (see Figure 1.).

T. petersi differs from nitidus in having the proportionally larger tympanum, a slightly different voice and generally darker dorsal and ventral patterns. It has not been established that the ranges of these two overlap or even meet, but this may be due primarily to the inaccessability of critical areas to collectors. I presume that the ranges meet in the lower Balsas Basin and its upper slopes in northern Guerrero and southern Michoacan

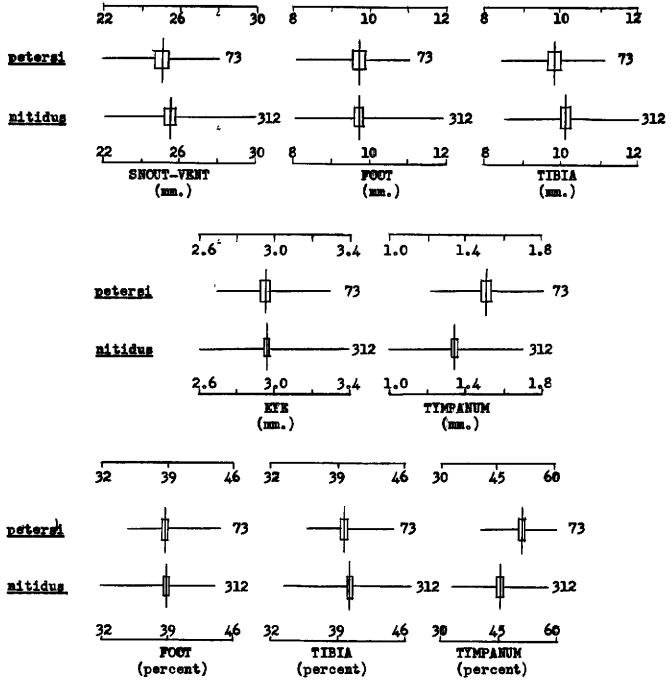


Fig. 1. Variations in size and proportions of T. nitidus and T. petersi. Vertical line represents mean; open rectangle twice the standard error; horizontal line the range in variation; number to right of horizontal line is the number of specimens used in the analysis. Figures for proportions of foot and tibia lengths are percentages of the snout-vent length; for tympanic width, percentage of eye diameter.

where the two have been collected at localities only 45 miles apart.

The above information indicates that there are closer relationships between these two than was formerly believed, and that *petersi* no longer warrants specific rank. I find it advisable to allocate *petersi* to a subspecific rank under *T. nitidus* and recognize this group as one polytypic species with two geographic races.

ACCOUNTS OF SPECIES AND SUBSPECIES

Tomodactylus nitidus nitidus (Peters)

Liuperus (sic) nitidus Peters (1869:878), original description

Tomodactylus amulae Gunther (1900:219)

Paludicola (Liuperus) nitidus, Parker (1927:451)

Tomodactylus nitidus, Kellogg (1932:120-123)

Tomodactylus nitidus, Taylor and Smith (1948:48-49)

Tomodactylus nitidus, Davis and Dixon (1955:154-155)

Type. One specimen, number 6669, Museum Nat. Berlin, Germany. Type locality: State of Puebla, probably near Matamoros, Puebla, Mexico.

Diagnosis. A grayish toad with the tips of the two outer fingers slightly to moderately expanded; snout-vent length 22.0 to 30.0 mm. (mean 25.5 mm.); tympanum relatively large (1.0 to 1.7 mm., mean 1.35 mm.), separated from eye by a distance less than or equal to tympanic width; yellowish or whitish spot on anterior and posterior faces of femur; venter immaculate or with a few dark spots.

Description. Maximum snout-vent length among 312 adult males, 30.0 mm., but average adult size only 25.5 mm.; general aspect somewhat toad-like with slender arms and legs (the small pustulations that roughen the skin enhance this

appearance); canthus rounded with no discernable ridge; tympanum relatively large, slightly less than one-half the width of eye; tarsal fold absent or indistinct; large subarticular tubercles; sole and palmar supernumerary tubercles minute; inner metatarsal tubercle somewhat larger than outer; first finger shorter than second; fourth toe considerably longer than third or fifth; fore and hind limbs relatively slender; tibiotarsal articulation reaches to anterior arm insertion or tympanum when leg is brought forward along side of body. When legs are folded at right angles to main axis the heels overlap; tips of two outer fingers slightly to moderately expanded; no vomerine teeth; tongue pear-shaped, notched behind and widest posteriorly; inner nares round or slightly oval and situated laterally; openings into the vocal sacs paired slits on inner edge of posterier half of jaw; inguinal gland low in groin, often inconspicuous by its coloration but always discernable, often subcircular in appearance and slightly to moderately elevated above surrounding skin.

In life the dorsal coloration is highly variable but the color pattern rarely so. The dorsal ground color varies from gray or cream to a dirty brown. On this is an extensive mottling of tan that may vary to olive green or dark brown. An interorbital bar of variable color, but always

lighter than surrounding color, is usually present. A dark canthal stripe passes from the nostril posteriorly through the eye and often to the tympanum. The fore and hind limbs have distinct bands usually the color of the dark dorsal coloration but sometimes tinted with yellow. These bands are slightly wider or of equal width to the light interspaces. The anterior and posterior faces of the femur and occasionally the groin have an immaculate spot of color that varies from yellowish white to deep yellow. The venter is usually grayish white with occasional brownish spots.

Individual Variation: Tomodactylus nitidus nitidus was selected for a study of individual variation because its wide range includes three major vegetation types and diverse topography. Eleven populations of this subspecies were subjected individually to statistical analysis to determine the extent of individual variation and subsequently of group variation. Of the 11 populations analyzed, one designated as the Taxco population, was selected for intensive study because of locality, habitat, range of elevation, and the number of individuals available.

The Taxco population occurs at elevations between 4,500 to 5,500 feet in a pine-oak community in which there are many areas cleared for agricultural purposes and exposed rocky hillsides. This is the typical habitat of T. nitidus

nitidus. A series of 52 adult males and 3 adult females was studied in the analysis. The females were not included in the mensural analysis because of the few specimens available. Characters and external measurements used in the analysis are as follows: Dorsal pattern; ventral pattern; inguinal gland; width of digits; tibiotarsal articulation; tympanic width; snout-vent length; foot length; tibia length; ratio of snout-vent to foot and to tibia; ratio of diameter of eye to tympanum; width of eye and of tympanum (see Table 1 and 2).

Age variation can be deleted in part from the analysis due to the fact that no juveniles were observed in this population. There were a few smaller individuals that appear to be subadults. It is possible in Tomodactylus, as in other cold-blooded vertebrates, that sexual maturity may be reached after individuals have attained only one-half or less of their potential size. If this be the case, ratios (proportions) rather than absolute sizes are of more value because some mensural characters are not increased after the structures are completely formed in the embryos or new born young. However, in this population the analyses of absolute sizes and ratios (Table 1) indicate that only a small amount of variation occurs in the absolute measurements of the snout-vent length, foot length, and tibia

length as compared to the same measurements expressed in proportions. Absolute measurements of the eye and the tympanum vary considerably (Table 1) but this may be due to the difficulty of measuring small objects (1-3 mm.) which could be termed "human error", or to the condition of the preserved specimens or both. Of the nine external measurements, only those of the eye and the tympanum are relatively variable. The others vary approximately five percent. The three females exhibit only slight mensural character differences from the males and these appear to be sex-linked. The tympanum is relatively larger in females, as are the general body proportions. There appear to be no differences in color or color pattern between the sexes.

Martin del Campo (1940) observed the incubation and hatching of eggs of T. nitidus nitidus and noted that the color pattern developed just prior to the hatching of the eggs. He found no differences between the color pattern of the young and that of the adults. There is, however, some degree of variance in the dorsal and ventral color pattern (Table 2) that may possibly be correlated with season. Seasonal variation is difficult to determine in Tomodactylus because of their secretive habits. They are seldom heard calling prior to the rainy season. Once the rainy season starts, breeding occurs for about two weeks and after that

only occasional breeding pairs are found. Tomodactylus call infrequently after the two weeks of breeding which makes the collecting of the animals very difficult during most of the year. The observed variation may also be due to slight genetic differences that exist between individuals of a population.

The amount of time involved in field and laboratory work did not afford me the opportunity to form any concrete opinions as to the occurrence of density-dependent and neurogenic variations. It is a well known fact that the latter type of variation occurs frequently among cold-blooded vertebrates but is is doubtful that neurogenic variation would occur in the small localized population reported on here. These seems to be no indication of genetic polymorphism or individual variants in the Taxco population.

Group Variation. Preserved specimens of 312 adult males and 18 adult females representing 11 populations were examined for group variation. The small number of females was not used in the statistical analyses. The 11 populations, herewith designated by associated towns, represent the theoretical range of distribution of T. nitidus nitidus. Extending generally from northwest to southeast, the populations are as follows: Copullo; Tuxpan; Cuautla; Progreso; Chilpancingo; Taxco; Alpuyeca; Acatlan; Acultzingo; Nochixtlan;

Table 1. Individual variation in the Taxco sample of *T. n. nitidus*, based on 52 adult males. Foot and tibia lengths are proportional (in percentage) to the snout-vent length. Tympanic width proportions are percentages of the eye diameter.

STATISTIC	S-V	FOOT		TIBIA		TYMPANUM		EYE
	mm.	mm.	%	mm.	%	mm.	%	mm.
Maximum	28.5	11.9	43.7	12.0	45.6	1.7	57.0	3.3
Minimum	23.0	8.6	36.3	9.1	34.7	1.0	33.3	2.6
Range	5.5	3.3	7.4	2.9	10.9	0.7	23.7	0.7
Mean	25.4	10.0	39.5	10.3	39.3	1.3	43.9	2.9
Standard Deviation	1.4	0.662	2.1	0.663	2.1	0.191	5.9	0.147
Standard Error of the Mean	0.191	0.092	0.3	0.090	0.3	0.026	0.8	0.024
S.E. of Standard Deviation	0.135	0.065	0.2	0.064	0.2	0.018	0.5	0.014
Variability %	5.3	6.6	5.3	6.4	5.3	14.0	13.0	5.0

Table 2. Individual variation of mensural characters and color pattern of the Taxco population of T. n. nitidus, based on 52 adult males. The variation is expressed in the number of individuals.

TIBIOTARSAL ARTICULATION		WIDTH OF DIGITS	
To Tympanum	21	Slight	12
To Arm Insertion	31	Moderate	40
To Eye	0	Great	0
TYMPANUM		INGUINAL GLAND	
Distinct	43	Distinct	50
Indistinct	9	Indistinct	2
WIDTH OF BARS ON LIMBS		INTERORBITAL BAR	
Narrow Interspaces	28	Distinct	48
Wide Interspaces	7	Indistinct	3
Equal Width	17	Absent	1
DORSAL MOTTLING		VENTRAL SPOTTING	
Bold	14	Many	3
Medium	21	Few	8
Light	17	Absent	41

and Oaxaca de Juarez.

Three major vegetational types are represented within the geographic range of these populations, as follows: Pine-oak Forest; Tropical Deciduous Forest; and Arid Tropical Scrub. In some instances the vegetation type inhabitated by the various populations is in disclimax because of agricultural practices. For the number of individuals observed in each population, elevation, and vegetation type refer to Table 3.

The differences between the 11 populations appear to be a combination of genetic and ecologic variations. There is considerable variance in absolute size and in proportions. The local environment of one population does not appear to integrade with neighboring ones to form a continuous gradient. This is perhaps due to the diverse topography and rapid replacement of vegetation types with changes in altitude. Each population is believed to be more or less adapted to the environment in which it lives. If the population is genetically variable there may be a selective factor advantageous to its existance in that particular habitat. The spacing between trees, rocks, and other cover within the habitat of one population may vary considerable throughout the range of the total population to increase the possibility of variation in length of leg, width of digits,

of eyes, and of tympanum. There are no indications of clines (see Fig. 3) between the eleven populations on the basis of the measureable characters. This is perhaps an indication of active species formation. Mayr (1942:97) states that the general rule for the presence of clines between populations is that the more clines found in a region the less active the species formation.

There appears to be a definite color gradient among the populations from the southeast to the northwest. The southeastern populations have light coloration while those of the northwest are much darker. This color gradient may be caused by neurogenic variation which Mayr, Linsley, and Usinger (1953:90) define as the color change in individual animals in response to the environment. The color pattern seems to be less variable than external measurements or color alone. The primary color gradients are found on the femur and dorsum (see Table 4).

The foregoing data have shown that in one population sample there is as much variation among individuals of the sample as there is among samples of the total population (refer to Tables 1 through 4 and Figures 2 through 5).

The Chilpancingo and Tuxpan populations merit special consideration because they deviate somewhat from the general variational pattern. The Chilpancingo population

differs from the others in having a much smaller tympanum. This population along with others that inhabit the arid Balsas Basin (Alpuyeca, Progreso, Taxco, and Acatlan) has a relatively longer tibia than those that inhabit the surrounding mountain slopes (Fig. 3). The Balsas Basin and its drainage system has primarily an arid tropical scrub vegetation type in the lowlands and a tropical deciduous forest along the upper slopes. There seems to be less plant cover for these populations which, in turn, requires that they travel greater distances for breeding, for feeding, and for hiding. A longer leg may be correlated with these activities.

The Tuxpan population seems to be developing rapidly towards geographic and reproductive isolation. It differs from other populations in the following characters: (1) proportionally shorter foot and tibia; (2) greater snout-vent length; (3) larger tympanum, both actually and in proportion to eye; (4) larger subarticular tubercles which are more conical in shape; (5) greater expansion of tips of two outer fingers; (6) darker ventral coloration (Figs. 3-5). This population occupies a geographic range of limited extent. It is closely bordered on the east, west, and south by other populations and for this reason I do not deem it advisable to name this population.

Range: Tomodactylus nitidus nitidus is confined

largely to the Balsas Basin, the Oaxacan Highlands, and the surrounding mountains from 1,500 feet to an elevation of 8,000 feet. The range includes all or parts of Veracruz, Puebla, Oaxaca, Morelos, Guerrero, Mexico, and Michoacan.

Habits: The habitat of this subspecies includes three major vegetation types. The animal is frequently found under stones during the daylight hours and at night seems to prefer to call from rock fences, low plant growth, or canyon walls. Its call is a single "peep" or "pee-ee-eep". At the height of breeding activities individuals frequently call from the ground, rocks, bushes, or even from trees as high as eight feet above the ground. It seems to show no preference to vegetation types and may be found climbing on cacti, thorny, broadleaf, and narrowleaf plants or even the trunks of trees.

Egg laying usually occurs under rocks where a little moisture is available. The incubation period is not known but is expected to be approximately 35 to 50 days. The several species of Tomodactylus, like other members of the family Leptodactylidae, have direct development. The females have no vocal sacs but are capable of emitting a shrill "peep" that is distinguishable from that of the males. The life expectancy is not known.

Locality Records: GUERRERO: 2.5 mi. S. Almolonga, 5,600 ft., (TCWC 15); 3 mi. W. Chilpancingo, 5,000 ft.,

(TCWC 1); 4 mi. W. Chilpancingo, 5,800 ft., (TCWC 3); 2 mi. S. Chilpancingo, 3,700 ft., (UMMZ 22); 2-5 mi. S. Chilpancingo, 3,500 ft., (UIMNH 4); 12 mi. S. Chilpancingo, 4,000 ft., (UIMNH 2); 1 mi. SW. Colotlipa, 2,700 ft., (TCWC 2); El Naranjo, 4,000 ft., (UIMNH 2); 12 mi. S. Iguala, 2,200 ft., (TCWC 6); Lake Tixtla, 4,400 ft., (UIMNH 1); Road to Omiltemi, 4,500 ft., (UIMNH 1); Palo Blanco, 3,800 ft., (UIMNH 1); Rio Balsas, near Mexcala, 1,500 ft., (TCWC 3, UIMNH 1); Taxco, 5,500 ft., (UMMZ 19); 2 mi. E. Taxco, 5,500 ft., (TCWC 6); S. of Taxco, 4,500 ft., (UIMNH 1); 8 km. N. Taxco, 5,500 ft., (TCWC 27); 17 km. S. Taxco, 4,000 ft., (TCWC 3); 0.5 mi. S. Tonalapan, 2,700 ft., (UIMNH 1).

MEXICO: Ixtapan de la Sal, 5,200 ft., (AMNH 7, CNHM 5); 4 mi. SE. Ixtapan de la Sal, 5,000 ft., (CNHM 1); 4 mi. N. Tenancingo, 7,600 ft., (TCWC 14); 5 mi. N. Tenancingo, 7,800 ft., (TCWC 1).

MICHOACAN: 1 mi. N. Copullo, 6,100 ft., (TCWC 1); 2.5 mi. N. Copullo, 6,300 ft., (TCWC 4); 5 mi. N. Copullo, 6,800 ft., (TCWC 10); 1.4 mi. SW. Tuxpan, 6,100 ft., (UMMZ 3); 2.7 mi. SW. Tuxpan, 6,400 ft., (UMMZ 5).

MORELOS: Alpuyeca, 3,500 ft., (TCWC 2); 3 mi. S. Alpuyeca, 3,500 ft., (TCWC 7); 12 km. NW. Axochiapan, 3,500 ft., (TCWC 17); 10-12 mi. NE. Cuautla, 6,500 ft., (TCWC 36); 2 mi. N. Cuernacava, 6,000 ft., (UIMNH 11);

8 mi. E. Cuernavaca, 4,800 ft., (UIMNH 3); Cuernavaca, 5,000 ft., (TCWC 1, USNM 5, UIMNH 4); El Rodeo, 3,500 ft., (TCWC 1); Huajintlan, 3,500 ft., (UIMNH 1); 2.4 mi. E. Huajintlan, 3,500 ft., (UMMZ 3); 2 km. S. Jonacatepec, e,500 ft., (TCWC 1); Progresso, 5,000 ft., (TCWC 21); Puente de Ixtla, 2,800 ft., (UIMNH 2); Tepoztlan, 6,100 ft., (TCWC 1, CNHM 1); 12 mi. W. Yautepec, 5,000 ft., (TCWC 1).

OAXACA: Cuicutlan, 1,800 ft., (UIMNH 2); 4 mi. NW. El Coyul, (67 mi. NW. Tehuantepec), 3,800 ft., (TCWC 6); 14 mi. N. Nochixtlan, 7,000 ft., (UKMNH 4); 7 mi. SE. Nochixtlan, 7,300 ft., (TCWC 1); Oaxaca de Juarez, 5,200 ft., (UMMZ 30); 8 mi. SE. Oaxaca de Juarez, 5,100 ft., (UMMZ 2); 6 mi. NW. Yanhuitlan, 7,700 ft., (TCWC 1); 3 mi. NW. Yanhuitlan, 7,500 ft., (TCWC 5); 1 mi. SE. Yanhuitlan, 7,000 ft., (TCWC 13).

PUEBLA: 3.5 mi. SE. Acatlan, 4,900 ft., (TCWC 8); 1.5 mi. NW. Cholulu, 6,700 ft., (UKMNH 2); Near Cacoloapan, 5,500 ft., (UIMNH 4); El Riego, 2 mi. W. Tehuacan, 5,500 ft., (CNHM 2); 8.5 mi. SW. Matamoros, 4,600 ft., (TCWC 9); Santa Catarina, 4,800 ft., (UIMNH 1); Tehuacan, 5,500 ft., (UIMNH 2).

VERACRUZ: Acultzingo, 7,000 ft., (UIMNH 1, USNM 1, UMMZ 4); Near Acultzingo, 7,000 ft., (UIMNH 2); El Chico (7 mi. SSE. Jalapa, 3,500 ft., (CNHM 5).

Table 3. Sample size, elevation, and vegetation type of eleven populations of *Tomodactylus nitidus nitidus*.

SAMPLE	NUMBER	ELEVATION	VEGETATION TYPE
Copullo	13♂ 2♀	6000 feet	Pine-oak
Tuxpan	8 0	6500 feet	Pine-oak
Cuautla	54 2	6000 feet	Pine-oak
Progreso	20 1	5000 feet	Tropical Deciduous
Chilpancingo	42 3	4500 feet	Arid Tropical
Taxco	52 3	5000 feet	Pine-oak
Alpuyeca	31 1	3500 feet	Arid Tropical
Acatlan	29 2	4000 feet	Arid Tropical
Acultzingo	6 2	7000 feet	Pine-oak
Nochixtlan	18 1	7000 feet	Pine-oak
Oaxaca de Juarez	37 1	5000 feet	Pine-oak

Table 4. Color gradients in eleven samples of *Tomodactylus nitidus nitidus*.

SAMPLE	FEMUR SPOT	DORSAL COLOR	VENTRAL SPOTS
Copullo	Deep Yellow	Dark Brown	Many
Tuxpan	Deep Yellow	Dark Brown	Many
Cuautla	Bright Yellow	Brown or Green	Moderate
Progreso	Yellow	Brown or Green	Few
Chilpancingo	Yellow	Brown or Green	Few
Taxco	Yellow	Brown or Green	Few
Alpuyeca	Yellow	Light Brown	Few
Acatlan	Yellow	Light Brown	Very Few
Acultzingo	Yellow	Tan to Brown	Very Few
Nochixtlan	Dull Yellow	Tan to Brown	Very Few
Oaxaca de Juarez	Yellow-white	Gray to Tan	None

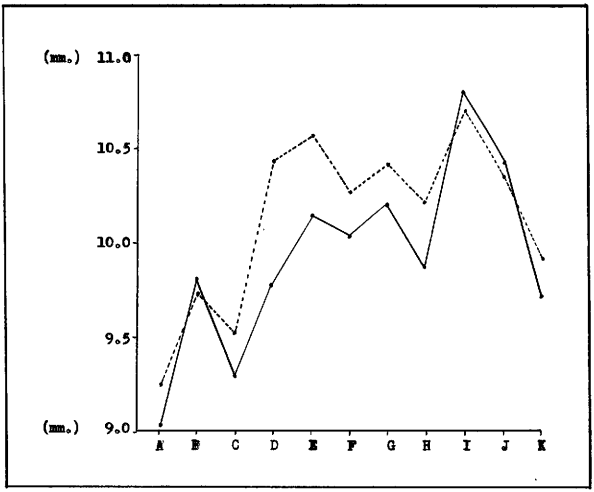


Fig. 2. Variations in mean length of the foot and tibia in the subspecies T. n. nitidus. The solid line connects the mean foot length; the dotted line, mean tibia length. The following populations are arranged in a line from northwest to southeast: A - Copullo; B - Tuxpan; C - Cuautla; D - Progreso; E - Chilpancingo; F - Taxco; G - Alpuyeca; H - Acatlan; I - Acultzingo; J - Nochixtlan; K - Oaxaca de Juarez.

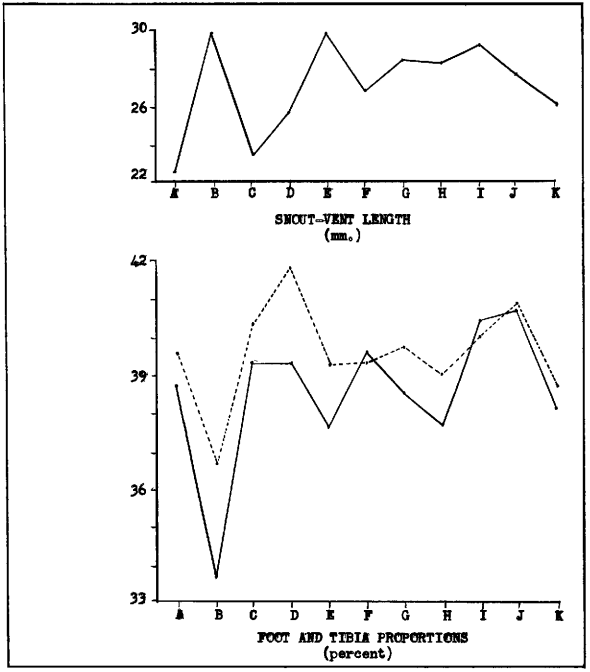


Fig. 3. Variations in the mean size and in proportions of T. n. nitidus. The solid line connects the mean snout-vent length and foot proportions; the dotted line connects the tibia proportions. Figures for proportions are percentages of the snout-vent length. The populations are as follows: A - Copullo; B - Tuxpan; C - Cuautla; D - Progreso; E - Chilpancinto; F - Taxco; G - Alpuyeca; H - Acatlan; I - Acultzingo; J - Nochixtlan; K - Oaxaca de Juarez.

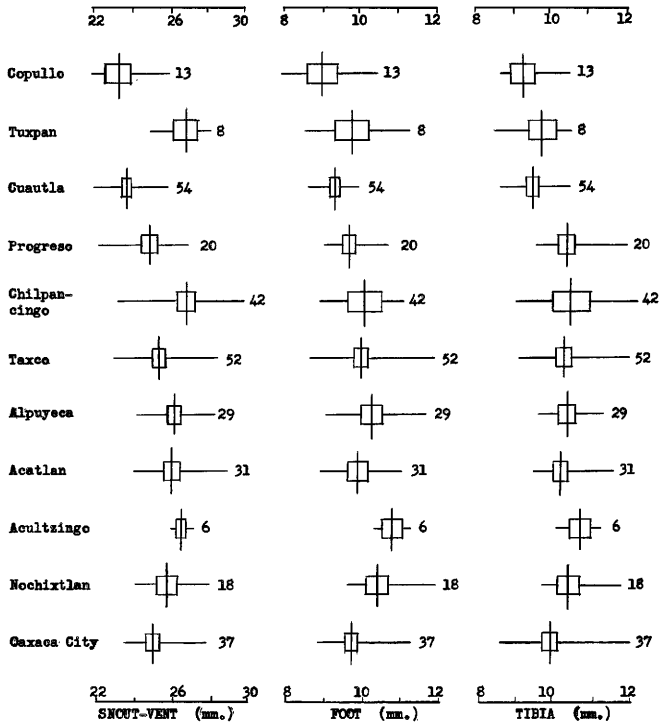


Fig. 4. Variations in size of samples of T. n. nitidus. The vertical line represents the mean; open retangle twice the standard error; horizontal line the range in variation. The number at the right of horizontal line is the number of specimens used in the analysis.

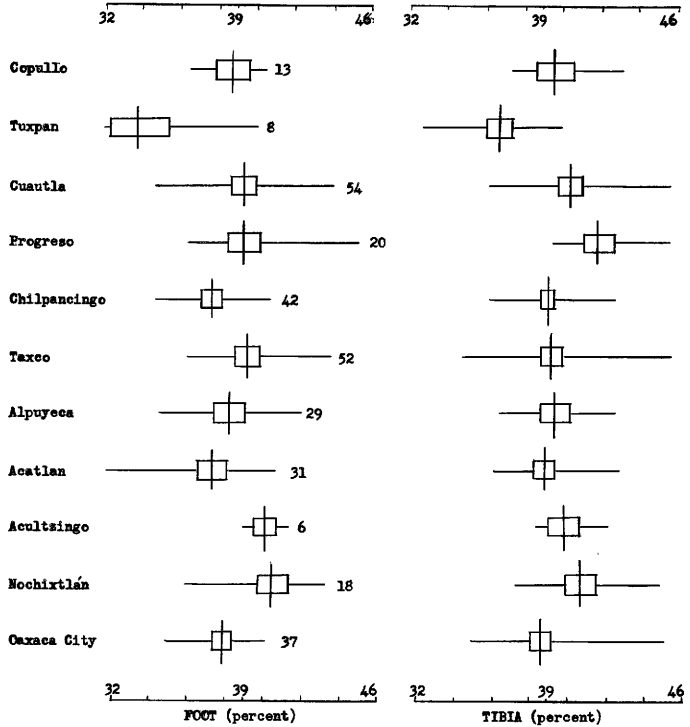


Fig. 5. Variations in proportions of T. n. nitidus. Vertical line represents the mean; open rectangle twice the standard error; horizontal line the range in variation. The number to the right of the horizontal line is the number of specimens used in the analysis. Figures for proportions are percentages of the snout-vent length.

Tomodactylus nitidus petersi Duellman

Tomodactylus petersi Duellman (1954:5-7), original description.

Type. Number 109238, University of Michigan Museum of Zoology. Type locality: One fourth mile east of Coalcoman, 3,500 feet, Michoacan, Mexico.

Diagnosis: A brownish toad with tips of two outer fingers moderately expanded; tympanum distinct and equal to one-half diameter of eye; patch on thighs and groin yellowish orange or orange; venter white with heavy spotting on chest that frequently continues onto belly; throat dark gray or frequently black.

Description: A moderately large Tomodactylus with an average snout-vent length of 25.0 mm. (range 22.0 - 28.0 mm.); tympanum relatively large, equal to one-half diameter of eye; canthus rounded but distinct; dorsum moderately pustular in life (not often visable in preservative); tips of two outer fingers moderately truncate, third finger longer than second or fourth; tibiotarsal articulation reaches to anterior arm insertion or to tympanum, rarely to eye; tarsal fold absent; no webs connecting digits of hands or feet; sub-articular tubercles large, high, and rounded; with legs folded at right angles to main axis of body the heels slightly overlap; head slightly narrower than body; tongue pear-shaped,

frequently notched behind and free for half its length; vocal sacs open by paired slits along inner edge of jaw. The females, like those of T. nitidus nitidus, appear to have no vocal sacs. They have a larger tympanum and body.

In life the dorsal ground color varies from grayish tan or greenish gray to dark brown. The darker mottling varies from olive green or brown to black. The bands on the fore and hind limbs are usually the color of the mottled pattern and wider than the light interspaces. Occasionally the light interspaces are very narrow, especially in specimens from the northern parts of the range. The lips are spotted with silvery white which occasionally forms a wavy line to posterior corner of jaw. The interorbital bar is frequently obscured by the dorsal coloration. The immaculate patch of color on the faces of the femur and in the groin varies from orange yellow to bright orange. The ventral color varies from white to bluish white with heavy spotting of brown or black. The throat in most is bluish gray but infrequently varies to black.

Discussion: The same measurements and morphological characters used in the analysis of T. nitidus nitidus were also used in the study of this subspecies. In all, 83 males and 4 adult females were examined but only the adult males were used in the analyses. The analyses indicate

that approximately five per cent variation occurs in the length of head and body, foot, and tibia, width of eye and of tympanum; proportions of foot and tibia and of tympanum (Table 5). Qualitative characters such as color pattern, color, tibiotarsal articulation, and expansion of digits, indicated the same trend exhibited in T. nitidus nitidus. Ten juveniles were not included in the analysis of mensural characters.

Habits: The habitat of T. nitidus petersi is much like that of T. nitidus nitidus. It occurs in three major vegetation types; Pine-oak Forest, Tropical Deciduous Forest, and Arid Tropical Scrub. Much of the Sierra Madre Occidental highlands occupied by this subspecies is now in disclimax because of extensive cutting of timber and intensive agricultural use. There are many semi-bare hillsides with only a scant growth of thorny plants or scrub oak that were once covered by dense forests of pine. What effects this change may have had on Tomodactylus are unknown. Tomodactylus n. petersi seems to show no preference for a particular type of vegetation in which to climb, to hide, or to call. In this respect it is similar to nitidus nitidus. During the breeding season the animal may be found dalling from the ground, rocks, shrubs, and trees. The breeding season varies with the time of the rainy season but is usually a week or two

later than in nitidus nitidus. Where the ranges of the two are in close proximity, breeding takes place at the same time. I assume that this subspecies, like nitidus nitidus, lays its eggs under rocks some time during the rainy season. The incubation period is not known. A juvenile 12 mm. in length was collected on August 12, which indicates an incubation period of about seven weeks, presuming the rainy season and breeding begin about the first two weeks of June.

Range. Tomodactylus n. petersi is restricted largely to the lower Balsas valley and its upper slopes and to the Pacific coastal slopes to the western and southwestern edge of the Mexican Plateau. The geographic range includes the following states: northern Guerrero, Michoacan, Colima, Jalisco, Nayarit, eastern Sinaloa, and probably extreme western Guanajuato. The lower coastal regions are not occupied by this species.

Locality Records. GUANAJUATO: No specific locality, (BMNH 1).

GUERRERO: El Limon, 2,500 ft., (USNM 1).

JALISCO: 11 mi. NW Amatitlan, 4,000 ft., (TCWC 1); 8 mi. S. Autlan, 2,800 ft., (UIMNH 1); 40.2 mi. S. Guadalajara, 5,000 ft., (FAS 1); 5 mi. S. Guadalajara, 5,100 ft., (TCWC 5); 18 mi. NW Guadalajara, 4,500 ft., (UIMNH 6); Magdalena, 4,500 ft., (UIMNH 2); 8 mi. S. Santa Cruz, 5,200 ft., (TCWC 3);

Zapotiltic (Magdalena), 4,500 ft., (UIMNH 3).

MICHOACAN: 4.7 mi. E. Apatzingan, 1,100 ft., (UMMZ 3); 3.4 mi. W. Apatzingan, 1,100 ft., (UMMZ 5); Cerro Guzman, near Coalcoman, 3,500 ft., (UMMZ 2); 1.2 mi. S. Charapendo, 3,000 ft., (UMMZ 5); 0.4 mi. E. Coalcoman, 3,500 ft., (UMMZ 3, TCWC 1); El Sabino, 5,000 ft., (UIMNH 1); Hacienda la Playa (Jorullo Volcano), 2,800 ft., (UMMZ 2); 20 mi. E. Jiquilpan, 6,200 ft., (TCWC 1); 12 mi. S. Tzitzic, 5,000 ft., (UIMNH 1); Uruapan, 5,200 ft., (UIMNH 3); North slope Volcan Jorullo, 3,000 ft., (UMMZ 1); Zamora, 5,200 ft., (UIMNH 1).

NAYARIT: 2 mi. NW Ahuacatlan, 2,900 ft., (TCWC 1); El Ocotillo, 2,300 ft., (AMNH 1); 15.2 mi. W. Ixtlan del Rio, 3,400 ft., (FAS 1); 30 mi. SE Tepic, 3,000 ft., (TCWC 3); 1 mi. NW Tepic, 3,100 ft., (TCWC 2); 3 mi. NW Tepic, 2,900 ft., (UMMZ 9); 6.7 mi. N. Tepic, 2,700 ft., (FAS 3).

SINALOA: 49 mi. NE Concordia, 4,800 ft., (RWA 2).

Table 5. Variation of mensural characters of T. n. petersi, based on 73 adult males. Foot and tibia length proportions are percentages of the snout-vent length. Tympanic proportions are percentages of the eye diameter.

STATISTIC	S-V	FOOT		TIBIA		TYMPANUM		EYE
	mm.	mm.	%	mm.	%	mm.	%	mm.
Maximum	28.0	11.0	44.2	11.1	44.2	1.8	60.0	3.3
Minimum	22.0	8.0	35.2	8.4	36.1	1.2	40.0	2.7
Range	6.0	3.0	9.1	2.7	8.1	0.6	20.0	0.6
Mean	25.0	9.7	38.9	9.8	39.3	1.5	50.6	2.95
Standard Deviation	1.4	0.598	1.8	0.594	1.8	0.110	3.1	0.115
Standard error of the Mean	0.163	0.070	0.2	0.070	0.2	0.013	0.4	0.013
S.E. of Standard Deviation	0.115	0.050	0.15	0.050	0.12	0.009	0.3	0.009
Variability %	5.5	6.2	4.5	6.1	4.6	7.0	6.0	3.7

Tomodactylus orarius[1] sp. nov.

Holotype. Adult male, number 11154, University of Michigan Museum of Zoology, collected August 9, 1956, 4.5 mi. southwest of Tecolapa, 450 feet, Colima, Mexico, by William E. Duellman and Richard E. Etheridge.

Paratypes. Twelve specimens: UMMZ 104394 (2), 104397, 0.5 miles SW La Placita, 75 feet, Michoacan; UMMZ 104396, 1 mile N. Pomaro, 700 feet, Michoacan; UMMZ 11152-53, from the type locality; UMMZ 11165-66, 2 miles SW Colima, 1,500 feet, Colima. UIMNH 16019, Hacienda del Rio, 50 feet, Colima; UIMNH 16020-21, Manzanillo, 10 feet, Colima. AMNH 12552, before reaching Las Chivas, 300 feet, Nayarit.

Diagnosis. A member of the nitidus group of the genus Tomodactylus but differs from all other known members of that group in having significantly shorter hind legs. Differences in voice, tympanic width, and color pattern will serve as additional characters to distinguish it.

Description of Holotype. Snout-vent length, 25.0 mm.; tibia length, 9.5 mm. (38.0 per cent of snout-vent length); foot length, 9.2 mm. (36.8 per cent of snout-vent length);

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[1] In allusion to the coastal position of its geographic range.

interorbital width, 3.0 mm.; diameter of eye, 3.0 mm.; diameter of tympanum, 1.4 mm. (46.6 per cent of eye diameter); internarial distance, 2.2 mm. Snout short and rounded; diameter of eye slightly longer than its distance from nostril; canthus rounded and distinct; tympanum distinct, higher than long, and separated from the eye by a distance less than its diameter; choanae large, situated laterally; vocal sacs present, the openings elongate and located along inner edge of lower jaw; tongue pear shaped, free for half its length; digits of hands and feet without webs; arms slender; tips of outer two fingers with distinct truncate disks, wider than remainder of digit; median palmar tubercle large, outer one less than one-fourth as large. Length of fingers from the shortest to longest 1-2-4-3, toes 1-2-5-3-4. No tarsal fold; legs short; tibiotarsal articulation when brought forward reaches posterior arm insertion; with legs folded at right angle to body, the heels barely touch; tips of toes slightly widened and truncate; sole with very small but distinct tubercles, inner metatarsal tubercle twice size of outer one.

Skin of head with few scattered tubercles, back relatively smooth in alcohol although pustules can easily be discerned. A large subcircular inguinal gland present, low in waist, and slightly elevated above surrounding skin;

sides with large flat granules; skin of throat and breast smooth but abdomen granular.

In preservative the dorsal ground color is light grayish tan. On this is a mottling of grayish brown. An irregular grayish stripe extends from head to anus along the middorsal line. The amount of mottling decreases on the sides, fading into the grayish ventral color. The lips are grayish with scattered white spots. There are two indistinct bands of grayish tan on the forearm, narrower than the light interspaces. There are six indistinct bands of grayish tan on legs, considerably narrower than the light interspaces. The groin and anterior face of femur are yellowish white. The ventral surfaces are dirty gray and without spots. The throat is slightly darker than rest of venter.

Variation. An analysis of individual variation of the males in the type series shows approximately five per cent variability among the measurable characters (Table 6). Of the type series, two are females and eleven are males. The females have longer legs and a larger tympanum than the males but are smaller in snout-vent length. The vocal sac (throat) of the males varies from dirty gray to dark gray. The dorsal color pattern varies from a mottled to a spotty appearance. The bands of the fore and hind limbs are much narrower than the light interspaces in most of the type series. Only one

individual exhibits any ventral spotting; in all others the venter is immaculate.

Remarks. The following notes were taken by William E. Duellman in the field and are based on living animals: "Colima: 4.5 mi. SW of Tecolapa, 450 ft., August 9, 1956. Gray above with brown mottling. Venter dirty white. Thighs, anteriorly and posteriorly, bright deep yellow. Iris pale golden. Call, a soft Braaaa, sometimes followed by three high notes, Braaaaeep-ee-eep. Calling from bushes."

Comparison. Tomodactylus orarius differs from T. n. nitidus in lighter dorsal coloration; proportionally smaller tympanum; shorter legs; voice a bleat rather than a peep. Differs from T. nitidus petersi in lighter dorsal coloration, smaller tympanum, shorter legs, smaller hands, no ventral spots, voice a bleat rather than a trill or peep, yellow rather than yellow-orange or orange inguinal and femoral spots. Differs from T. angustidigitorum, T. grandis, and T. fuscus chiefly in femoral and groin color which is yellow rather than uniform brown; mottled or spotty dorsal color pattern, rather than unicolor; expanded tips of digits, rather than narrowed tips of digits (only in angustidigitorum and grandis). Differs from T. dilatus in yellow rather than ochraceous femoral and groin spots; ventral surface dirty gray, rather than pigmented and dotted with white flecks;

tips of two outer fingers slightly expanded, rather than twice the width of narrowest part of digit. Differs from T. albolabris in having shorter legs; white spots on upper lip rather than white line; a yellow rather than orange inguinal and femoral spot; dorsal color pattern mottled or spotty rather than unicolor.

Habits. I have not observed this toad other than as preserved material. I presume the habits of the animal to be much like that of other members of the T. nitidus group.

Range. This species is confined to the lower elevations along the Pacific Coast from the state of Nayarit southward to central Michoacan.

Locality Records. COLIMA: 2 mi. SW Colima, 1,500 ft., (UMMZ 2); Hacienda del Rio, 50 ft., (UIMNH 1); Manzanillo, 15 ft., (UIMNH 2); 4.5 mi. SW Tecolapa, 450 ft., (UMMZ 3 including holotype).

MICHOACAN: 0.5 mi. SW La Placita, 75 ft., (UMMZ 3); 1 mi. N. Pomaro, 700 ft., (UMMZ 1).

NAYARIT: Before reaching Las Chivas, 300 ft., (AMNH 1).

Table 6. Individual variation analysis of Tomodactylus orarius based on 11 adult males. Foot and tibia proportions are percentages of the snout-vent length. Tympanic proportions are percentages of the eye diameter.

STATISTIC	S-V	FOOT		TIBIA		TYMPANUM		EYE
	mm.	mm.	%	mm.	%	mm.	%	mm.
Maximum	26.3	9.8	39.6	10.0	40.9	1.6	53.3	3.0
Minimum	22.0	8.4	34.6	8.0	34.8	1.1	40.0	2.7
Range	4.3	1.4	5.0	2.0	6.1	0.5	13.3	0.3
Mean	24.7	9.2	37.3	9.3	37.8	1.4	46.9	2.97
Standard Deviation	0.974	0.374	1.4	0.506	1.7	0.16	4.3	0.09
Standard Error of the Mean	0.310	0.118	0.4	0.160	0.5	0.05	1.4	0.003
S.E. of Standard Deviation	0.220	0.084	0.3	0.113	0.4	0.04	0.9	0.002
Variability %	5.6	4.1	3.7	6.1	4.5	11.0	9.0	3.0

Tomodactylus dilatus Davis and Dixon

Tomodactylus dilatus Davis and Dixon (1955:155-157), original description.

Type. Number 11245, Texas Cooperative Wildlife Collection. Type locality: 4 miles west Mazatlan, 7,400 feet, Guerrero, Mexico.

Diagnosis: A relatively large grayish to brownish toad (23 mm. to 30 mm. in snout-vent length), which differs from all other known members of the genus in having a significantly smaller tympanum (37.6 per cent of eye diameter); tips of two outer fingers conspicuously truncate, twice the width of narrowest part of digit; relatively long legs; ochraceous spot in groin and on anterior and posterior faces of femur.

Description. A large member of the genus with a relatively small tympanum (mean 1.06 mm., range 1.0 mm. to 1.5 mm.); mean snout-vent length 25.4 mm., range 23.2 mm. to 28.8 mm. in males (29.3 mm. in single female); legs long, tibiotarsal articulation reaches beyond tympanum when leg brought forward along side of body; heels overlap when legs are folded at right angles to body; tips of toes expanded, innermost one barely so; hands large, tips of two outer fingers conspicuously widened and truncate; three palmar tubercles, median one largest; no tarsal fold; snout rounded;

canthus sharp-angled; tongue pear shaped, rounded behind and free for half its length; inner nares large, situated laterally; vocal sac openings large; skin of back heavily pustular, head usually with five longitudinal rows of tubercles; median dorsal dermal fold usually present; venter moderately granular; inguinal gland large, conspicuous, low in groin, and long as humeral region of arm; color pattern mottled; number of bands on fore and hind limbs variable; distinct loreal stripe present, from snout through nostril and eye to arm insertion; interorbital bar present.

The dorsal ground color grayish or grayish green; darker mottling brownish or greenish; loreal stripe dark brown; interorbital bar ground color; arm and leg bands brown to dark brown, lighter interspaces ground color; femur and groin with ochraceous spot; venter pigmented grayish brown with scattered white flecks; chin with few white spots on outer edge and along lower jaw; throat usually darker than ventral coloration.

Variation. The ventral pigmentation varies from grayish to grayish brown; dorsal mottling color varies from grayish green to dark brown; arm and leg bands usually eight in number but varies to five; dorsal dermal fold persent in most; five row of tubercles on head varies considerably, often becoming invisible in preserving fluid. The mensural

characters of 28 adult males vary about six per cent (Table 7). The single adult female is larger in snout-vent length and has a greater tympanic width.

Comparison. Tomodactylus dilatus differs from all other related species in having a small tympanum and an ochracreous spot in groin and on femur. Differs from all other known species (except T. fuscus and T. albolabris) in having the tips of the two outer fingers conspicuously truncate and dilated laterally. Differs from most members of the genus (except T. grandis) in having proportionally longer legs. Differs from T. fuscus and T. grandis chiefly in mottled color pattern and ochraceous femur and groin spots rather than a uniform color pattern.

Habits. This species seems to prefer wooded areas rather than a semi-open rocky habitat. I have not observed T. dilatus calling or hiding in a rocky habitat, but I have collected it in the mountains west of Mazatlan, Guerrero, among shrubs and pine trees from two to seven feet above the ground. There appears to be no preference of plant growth in which to call. In one night of collecting, several individuals were taken from various types of leaves. None was found calling from the ground. The call of the male is a high pitched peep or trill that varies from three to five notes.

The breeding season begins in early June (varies with the rainy season) and continues for about three weeks. On June 7, a female was found to contain 68 eggs in various stages of development.

Range. Tomodactylus dilatus is largely confined to the mountains of west-central and northwestern Guerrero. Although the animal has been taken only from two areas near Chilpancingo, I presume the range covers most of the northwestern spurs of the Sierra Madre del Sur at elevations between 7,000 and 8,500 feet.

Locality Records. GUERRERO: 4 mi. W. Mazatlan, 7,800 ft., (UMMZ 2, TCWC 14); 2 mi. W. Omiltemi, 7,900 ft., (TCWC 1, UMMZ 1); 2 mi. SW Omiltemi, 7,900 ft., (TCWC 4); Omiltemi, 7,900 ft., (USNM 1, UIMNH 4, TCWC 9).

Table 7. Analysis of individual variation of Tomodactylus dilatus based on 28 adult males. Foot and tibia proportions are percentages of the snout-vent length. Tympanic proportions are percentages of diameter of eye.

STATISTIC	S-V	FOOT		TIBIA		TYMPANUM		EYE
	mm.	mm.	%	mm.	%	mm.	%	mm.
Maximum	28.8	11.2	47.0	11.6	47.4	1.5	50.0	3.6
Minimum	23.2	9.2	36.4	9.6	36.9	1.0	30.0	2.7
Range	5.6	2.0	10.6	2.0	10.5	0.5	20.0	0.9
Mean	25.4	10.3	40.5	10.7	41.9	1.06	37.6	2.84
Standard Deviation	1.24	0.556	3.1	0.494	2.87	0.072	4.9	0.085
Standard Error of the Mean	0.234	0.105	0.58	0.093	0.54	0.014	0.92	0.016
S.E. of Standard Deviation	0.116	0.074	0.40	0.066	0.38	0.009	0.65	0.011
Variability %	4.8	4.9	7.6	4.6	6.8	6.5	13.0	3.0

Tomodactylus albolabris Taylor

Tomodactylus albolabris Taylor (1943:351-353), original description.

Type. Number 29568, Edward H. Taylor - Hobart M. Smith Collection. Type locality: Agua del Obispo, km. 351, 3,300 feet, Guerrero, Mexico.

Diagnosis. A small member of the genus that differs from all other known members in having a slender body and proportionally long legs. Tips of two outer fingers distinctly widened and truncate, nearly twice the width of narrowest part of digit; red or reddish orange spot on anterior and posterior faces of femur and in groin; white line on upper lip; tibiotarsal articulation reaches tympanum or eye.

Description. A small slender species with the tips of the two outer fingers distinctly truncate and conspicuously dilated laterally; arms slender, hands small; three palmar tubercles present, median tubercle four times larger than outer two; subarticular tubercles large, conical in shape; numerous small granules on palm; legs long, slender; foot and tibia 79 per cent of snout-vent length; tibiotarsal articulation reaches tympanum or eye; sole of foot with minute granules; toes truncate but not distinctly widened; first toe small, contained in fourth toe over four times;

subarticular tubercles of inner toe larger than those of outer toes; inner metatarsal tubercle twice the size of outer one.

Mean snout-vent length of males 22.8 mm. (range 21 mm. to 26 mm.); mean snout-vent length of females 25.4 mm. (range 24 mm. to 27 mm.); snout pointed, tip slightly rounded; canthus rounded but not distinct; eye small, tympanum small (46 per cent of eye diameter); vocal sacs large, their openings located on floor of mouth near inner edge of jaw rami; inner nares large; tongue pear-shaped, tip rounded, and free for half its length; dorsal surface pustular; belly granular; inguinal gland distinct and elongate; color pattern of back usually concolor; ventral pattern variable, with or without spots.

The dorsal color is olive, olive brown or reddish; venter is usually white or creamy yellow with scattered dark brown or black spots; limbs with spots of dark brown contrasting with dorsal coloration; upper lip with white or silvery line; dark brown loreal stripe from nostril to eye; few scattered brown spots on sides; chin of males with occasional brownish pigment; inguinal gland mostly black with infrequent spots of dorsal coloration.

Variation. The mensural characters of 42 adult males vary about six per cent (Table 8). Females are larger than

males in most measurable characters. The dorsal color pattern varies from concolor to an indistinct mottling; ventral pattern varies from immaculate to scattered dark spots that may be diffuse or distinct. The dorsal color varies from olive to reddish brown; the venter from white to creamy yellow with brown or black spots diffuse, distinct, or absent.

A specimen of Tomodactylus collected by Ralph W. Axtell at the type locality of T. albolabris does not agree with the characters mentioned above. Davis and Dixon (1955:156-157) reported on this specimen and referred the animal to T. petersi until further evidence became available. After reviewing the characters exhibited by this toad I believe Davis and Dixon to be in error, even though additional information has not become available. The overall proportions of the body and its extremities are distinctly related to albolabris. The dorsal and ventral color and the color pattern tends to support this association even though they are distinct from the typical albolabris color and color pattern. The dorsum is almost black rather than olive or reddish brown and the venter is heavily spotted with dark brown rather than immaculate or with scattered dark spots. The upper lip is spotted with white rather than with a white line. The tips of the two outer fingers are truncate and slightly dilated laterally but not to the extent found in

albolabris. The voice consists of a "buzz" rather than a "peep or whistle".

On the basis of the animal's relationship to albolabris, the distinct voice unlike any other Tomodactylus, and the fact that the toad was collected in the same habitat with T. albolabris, I think it is best to allocate this animal to albolabris as an aberrant individual.

Comparison. Tomodactylus albolabris differs from most of the other known members of the genus in having proportionally longer hind limbs and a more slender body. Differs from T. orarius, T. nitidus and its subspecies in having a concolor dorsal color pattern rather than a distinct mottled pattern. Differs from T. angustidigitorum, T. fuscus, and T. grandis in having a red or orange spot in groin and on femur rather than groin and femur concolor, tips of two outer fingers conspicuously expanded rather than tapering and narrowest at tips (except T. fuscus). Differs from T. dilatus in having a much slenderer body and red or orange spot in groin and on femur rather than a robust body and ochraceous femur and groin spot.

Habits. T. albolabris, like T. dilatus, does not inhabit rocky areas or similar cover. The animals seem to prefer trunks, branches, or leaves of trees, or tall shrubs. Taylor (1943:353) states that all of the type series, which

was collected in August, was taken from trees at various heights above the ground. He also indicated that most of the calls that were heard came from high trees. The fact that the animals were in high trees at this time of year indicates that the pattern of dispersal follows the general trend of all Tomodactylus by seeking inaccessible places to call from during the latter part of the rainy season.

During the height of the breeding season (early June) I collected albolabris from trees and shrubs two to 10 feet in height. None was collected on the ground. Dr. W. B. Davis, however, has collected this species on rocks at Acahuizotla, Guerrero. Of the 52 individuals examined four were females, all of which were gravid. Breeding pairs in amplexus were not observed but I presume the eggs are deposited on the ground beneath leaf debris or logs.

Range. The known range of T. albolabris is restricted to the pine-oak and tropical deciduous forests between the villages of Mazatlan, Agua del Obispo, and Acahuizotla, Guerrero. These villages are found along the western slope of the Sierra Madre del Sur at elevations between 2,700 and 4,000 feet.

Locality Records. GUERRERO: Acahuizotla, 2,800 ft., (TCWC 19); Agua del Obispo, 3,300 ft., (TCWC 21, UIMNH 6, UMMZ 3); 9 km. S. Mazatlan, 3,600 ft., (UIMNH 1).

Table 8. Analysis of individual variation of Tomodactylus albolabris based on 42 adult males. Foot and tibia proportions are percentages of the snout-vent length. Tympanic proportions are percentages of diameter of eye.

STATISTIC	S-V	FOOT		TIBIA		TYMPANUM		EYE
	mm.	mm.	%	mm.	%	mm.	%	mm.
Maximum	25.7	10.2	42.5	10.9	44.8	1.7	56.6	3.1
Minimum	21.4	7.4	34.0	8.3	36.2	1.1	36.6	2.6
Range	4.3	2.8	8.5	2.6	8.6	0.6	20.0	0.5
Mean	22.8	8.7	37.9	9.5	41.1	1.25	45.8	2.83
Standard Deviation	1.04	0.644	2.1	0.578	2.1	0.121	2.2	0.138
Standard Error of the Mean	0.161	0.100	0.32	0.089	0.32	0.018	0.34	0.020
S.E. of Standard Deviation	0.114	0.071	0.22	0.063	0.23	0.013	0.24	0.015
Variability %	4.5	7.4	5.6	6.0	5.1	9.6	4.8	4.8

Tomodactylus angustidigitorum Taylor

Tomodactylus angustidigitorum Taylor (1940:494-496), original description.

Type. Number 18640, Edward H. Taylor-Hobart M. Smith Collection. Type locality: Quiroga (northeastern end of lake Patzcuaro), 6,880 feet, Michoacan, Mexico.

Diagnosis. A small member of the genus that differs from all other related species (except T. grandis) in having terminations of fingers narrower than digits. Maximum known snout-vent length of males 27.2 mm. (range 21.0 mm. to 29.0 mm. including females). Inguinal gland distinct and removed from groin; limbs relatively short; femur and groin usually concolor.

Description. Head narrower than body, extremities somewhat stout; foot and tibia 78.6 per cent of snout-vent length; tibiotarsal articulation reaches arm insertion, at most, the tympanum; sole of foot with several large and numerous small tubercles; two metatarsal tubercles of equal size; subarticular tubercles conical; no tarsal fold; arm short and somewhat stout; tips of fingers tapering and narrow; subarticular tubercles large, not conical but rounded; median palmar tubercle large; snout blunt, sometimes rounded or pointed; tongue narrow, widened posteriorly,

and frequently notched at tip, free for half its length; vocal sac openings large; dorsum usually, roughly pustular; paratoid gland large, indistinct, extending from upper edge of tympanum to arm insertion; inguinal gland elongate, distinct, and moderately raised above surrounding skin; belly roughly granular; chin and breast usually smooth. Color pattern usually concolor with occasional barring of femur, tibia, and forearms; venter dusky with scattered white-tipped granules.

The dorsal color varies from pinkish tan to nearly black; ventral color varies from white with purplish brown spots to buff with white tipped granules; color of occasional bars on extremities varies from reddish brown to black; loreal stripe dark brown; inguinal gland varies from yellowish white marbled with black to reddish brown marbled with black.

Variation. Analysis of individual variation of 80 adult males shows a variation of six per cent among measurable characters (Table 9). Females are larger than males (mean snout-vent length 25.1 mm., range 22 mm. to 29 mm.) and have a larger tympanum, 47 per cent of eye diameter. The general body shape varies considerably but this may be due to the methods of preserving the animals. The bars of the extremities may be present or absent. Color is quite variable as indicated above.

Comparison. T. angustidigitorum differs from all other known related species except T. grandis in having tapering digits that are narrowest at the tip. Differs from T. fuscus in having subequal metatarsal tubercles rather than inner metatarsal tubercle conspicuously larger than outer; tapering digits rather than digits conspicuously widened and truncate at tip; tibiotarsal articulation reaching arm insertion rather than tympanum; venter usually light in color rather than brown or dark brown. Differs from T. grandis in having small rather than large robust body; small tympanum, 44.3 per cent rather than 56.8 per cent of eye diameter; narrow internarial width, 74 per cent rather than 86 per cent of eye diameter.

Habits. Schmidt and Shannon (1947:68-69) reported that several specimens were collected on the slopes of Mount Tancitaro at an elevation of 7,800 feet in woodland and fields. They found the majority of the toads on rocks although a few were collected from bushes, up to a height of five feet. Taylor (1940:496) stated that all specimens of the type series were found under stones or hopping about on the ground. Ralph Axtell and I collected 57 individuals near Quiroga, Michoacan, in a variety of habitats. They were found calling from the ground, rocks, grass, and shrubs up to a height of four feet.

Of these 57 specimens, 11 were females that contained eggs in various stages of development. Two pairs were found in amplexus beneath clumps of grass. The following observation was made by me on the breeding behavior of the species: "Voice-Actions. Both sexes call; the call being a short "peep." The female has a much higher pitch and can easily be distinguished from the male while both are calling. While observing a calling male and female about 10 feet apart, the following action took place -- The male sat upon a small rise in the soil and voiced a peep; the female answered; the male rotated in a 360 degree turn on the rise, voicing a peep about every 90 degrees until he was sure of the direction of the answering female. Having his bearing, he hopped off in the direction of the female, voicing his peep about every two feet. As the two became in close proximity, the peeps of the male became a short trill of about five notes which was repeated three to five times in rapid succession. Further observations were not made beyond this point."

Mr. Axtell and I took advantage of this behavior by placing several calling females in a sack and placing it on the ground. The females continued to call and as the unsuspecting males answered they were easily located by flashlight and captured.

Range. This species seems to be largely restricted

to the pine-oak forest along the southwestern edge of the Mexican Plateau in south central Michoacan, between elevations of 5,000 and 8,000 feet.

Locality Records. MICHOACAN: Angahuan, 7,000 ft., (UMMZ 4); 3 mi. E. Angahuan, 6,900 ft., (UMMZ 1); 9 mi. E. Angahuan, 6,600 ft., (UMMZ 1); 2 mi. E. Apo, Cerro Tancitaro, 6,800 ft., (UMMZ 1); 4 mi. E. Carapa, 6,700 ft., (USNM 1); 9.5 mi. S. Carapan, 6,700 ft., (UMMZ 1); 29.2 mi. S. Carapan, 6,000 ft., (UIMNH 13); 4.5 mi. WNW Cheran, 7,700 ft., (UMMZ 1); 1.5 mi. E. Corupu, 6,800 ft., (UMMZ 14); Cuseno Station, 6,500 ft., (UMMZ 14); El Soledad (Tancitaro), 7,500 ft., (CNHM 3); Mount Tancitaro, 6,000-7,500 ft., (CNHM 12); 2.4 mi. S. Paracho, 7,800 ft., (UMMZ 8); 4 mi. S. Paracho, 7,600 ft., (UMMZ 2); 2.1 mi. NE Paricutin, 6,600 ft., (UMMZ 1); Patzcuaro, 6,800 ft., (UMMZ 2); Pedregal (Tancitaro), 5,00 ft., (CNHM 2); Quiroga, 6,880 ft., (UIMNH 2); 3.5 mi. E. Quiroga, 7,600 ft., (TCWC 13); 5.5 mi. E. Quiroga, 7,800 ft., (TCWC 44); San Juan Parangaricutiro, 6,600 ft., (UMMZ 15); San Juan Parigaricutiro, 6,500 ft., (UMMZ 1); between Tzinzuntxan and Patzcuaro, 6,800 ft., (UMMZ 1); Uruapan, 5,200 ft., (UIMNH 4); 4 mi. E. Uruapan Road, 5,400 ft., (UIMNH 4); Volcan Paricutin, 6,500 ft., (UMMZ 1); Zacapin, 5,200 ft., (UIMNH 2); 9 mi. W. Zacapu, 6,800 ft., (UIMNH 9); Zuitzingo (Tancitaro), 7,500 ft., (CNHM 18, USNM 1).

Table 9. Analysis of individual variation in Tomodactylus angustidigitorum based on 80 adult males. Foot and tibia proportions are percentages of the snout-vent length. Tympanum proportions are percentages of the eye diameter.

STATISTIC	S-V	FOOT		TIBIA		TYMPANUM		EYE
	mm.	mm.	%	mm.	%	mm.	%	mm.
Maximum	27.2	10.9	46.5	10.2	43.1	1.8	56.0	3.2
Minimum	21.0	7.6	33.3	8.0	34.2	1.0	36.6	2.5
Range	6.2	3.3	13.2	2.2	8.9	0.8	19.4	0.7
Mean	23.0	9.04	39.4	8.94	39.2	1.23	44.3	2.95
Standard Deviation	1.3	0.460	2.1	0.518	1.4	0.150	4.5	0.167
Standard Error of the Mean	0.148	0.050	0.240	0.060	0.16	0.017	0.38	0.018
S.E. of Standard Deviation	0.105	0.036	0.160	0.041	0.10	0.012	0.20	0.013
Variability %	5.6	4.5	5.3	5.8	3.5	12.0	10.0	5.6

Tomodactylus fuscus Davis and Dixon

Tomodactylus fuscus Davis and Dixon (1955:157-158), original description.

Type. Number 11252, Texas Cooperative Wildlife Collection. Type Locality: 1.5 miles southeast Huitzilac, 7,800 feet, Morelos, Mexico.

Diagnosis. Smallest member of the T. angustidigitorum group, with tips of fingers conspicuously expanded and truncate; eye small; venter usually brown. Dorsum roughly pustular; inguinal gland elongate, distinct; anterior and posterior faces of femur uniformly brown; occasional bars on extremities obscure.

Description. Smallest member of genus (average snout-vent length of males 22.2 mm., range 20.5 mm. to 25.0 mm.; of females, average 24.0 mm., range 23.0 mm. to 27.0 mm.); legs relatively long, tibiotarsal articulation reaches tympanum or eye; foot 39 per cent of snout-vent length; tibia 42 per cent of snout-vent length; sole of foot with numerous small tubercles and several large ones; outer metatarsal tubercle one-half as large as inner; subarticular tubercles large, conical; no tarsal fold. Hands small, tips of two outer fingers conspicuously expanded, truncate; median palmar tubercle four times larger than ones at bases of

first and fourth fingers; subarticular tubercles somewhat rounded; no trace of a tarsal fold.

Snout rounded or blunt; tympanum small, often indistinct, 45.5 per cent of eye diameter; tongue pear-shaped, often notched behind; vocal sac openings large; interorbital bar obscure; loreal stripe indistinct; parotoid gland large, subcircular, at upper posterior edge of tympanum; inguinal gland elongate or oval, removed somewhat from groin; skin of back pustular; venter roughly granular. Dorsal color pattern concolor or indistinctly mottled; ventral color pattern usually concolor or faintly spotted; bars of extremities obscure. Dorsal color brown to dark brown; venter light brown, sometimes stippled with black; loreal stripe, when discernable, dark brown.

Variation. Of the 31 adult males examined for an analysis of individual variation, only a small degree of variance was found among the measurable characters (Table 10). Examination of seven adult females revealed that they possessed a larger body (mean snout-vent length 24.0 mm.) and larger tympanum (mean tympanic width 1.46 mm.). The expansion of the tips of the two outer fingers varies from one and a half to nearly twice the width of the narrowest part of the finger. The coloration of this species is variable but is always brownish.

Comparison. Tomodactylus fuscus differs from all other members of the angustidigitorum complex in having the tips of the two outer fingers distinctly expanded and truncate; eye small; internarial width 80 per cent of eye diameter; legs longer in animals of comparable body size; and ventral surface brown. Differs from all other known species of Tomodactylus in having femur and groin concolor rather than with yellow, ochraceous, orange, or red spots; venter brownish rather immaculate with or without spots, or grayish with whitish subcircular spots; leg and arm bars obscure rather than distinct.

Habits. This species inhabits the pine-oak forest. The animals may be found calling from rocks, grass, shrubs, or trees and seem to show a preference for open woodland. The majority of the specimens that I have collected were found in abandoned corn fields that had become overgrown with weeds and shrubs. Most of the animals were found calling from shrubs rather than from rocks. In August of 1949, Dr. W. B. Davis, R. W. Axtell, and I spent three hours collecting two calling males. However, at this time of year the calls are infrequent, deceptive, and consists of a single peep or whistle. During the height of the breeding season, they are heard more frequently and are easier to capture. All of the females examined contained eggs in

various stages of development.

Range. The known range of T. fuscus appears to be confined to the pine-oak forest between elevations of 7500 and 8800 feet on the southern slopes of the mountains that form the southern edge of the Mexican Plateau. This range includes the states of Morelos, Mexico, and Michoacan.

Locality Records. MEXICO: 4 mi. N. Tenancingo, 7,600 ft., (TCWC 4); 6.5 mi. N. Tenancingo, 7,800 ft., (TCWC 2).

MICHOACAN: 9 mi. N. Copullo, 21 mi. E. Morelia, 7,500 ft., (TCWC 1); 15 mi. E. Morelia, 7,300 ft., (UMMZ 1).

MORELOS: 1.5 mi. SE Huitzilac, 7,800-8,000 ft., (TCWC 8); 5 km. N. Tepotztlan, 7,500 ft., (AMNH 8); Tres Marias, 7,500 ft., (UIMNH 6).

Table 10. Analysis of individual variation of Tomodactylus fuscus based on 31 adult males. Foot and tibia proportions are percentages of the snout-vent length. Tympanic proportions are percentages of diameter of eye.

STATISTIC	S-V	FOOT		TIBIA		TYMPANUM		EYE
	mm.	mm.	%	mm.	%	mm.	%	mm.
Maximum	25.0	9.8	43.8	11.0	45.7	1.6	53.3	3.1
Minimum	20.5	8.2	34.3	8.8	36.0	1.0	36.0	2.6
Range	4.5	1.6	9.5	2.2	9.7	0.6	17.3	0.5
Mean	22.2	8.78	39.3	9.13	41.9	1.27	45.5	2.8
Standard Deviation	1.26	0.447	2.2	0.482	2.0	0.126	3.8	0.146
Standard Error of the Mean	0.226	0.080	0.40	0.086	0.36	0.023	0.69	0.026
S.E. of Standard Deviation	0.160	0.057	0.28	0.060	0.26	0.016	0.49	0.018
Variability %	5.6	5.1	5.6	5.2	4.7	9.0	8.3	5.2

Tomodactylus grandis[1] sp. nov.

Holotype. Adult male, number 12628, Texas Cooperative Wildlife Collection, collected May 31, 1956, at San Pedro (2 miles south Tlalpam), 7,800 feet, Distrito Federal, Mexico, by James R. Dixon and Mary Dixon.

Paratypes. Thirteen males: TCWC 12629, from the type locality; UMMZ 99533 (11), 4 miles south Villa Alvaro Obregon, 7,600 feet, Distrito Federal; UIMNH 15987, Tlalpan, 7,600 feet, Distrito Federal.

Diagnosis. A member of the angustidigitorum complex that differs from all other known members of the group in having a large tympanum (56 per cent of eye diameter), large internarial width (86 per cent of eye diameter), and large size (average snout-vent length 28 mm.). Femur and groin concolor with scattered whitish flecks near knee; dorsal surface brown, pustular; ventral surface buff, granular; tips of two outer fingers tapering, narrowest at tip.

Description of Holotype. Snout-vent length 30.5 mm.; foot, 12.3 mm.; tibia, 11.6 mm.; length of inguinal gland, 7.5 mm.; width of head, 11.7 mm.; width of eye, 3.6 mm.;

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[1] In allusion to the large size.

tympanic width, 2.0 mm.; internarial width, 2.8 mm.; distance from eye to nostril, 3.0 mm.; dorsum pustular; venter heavily granular; head slightly narrower than body; snout blunt; canthus rounded; tympanic width greater than distance from eye to tympanum; parotoid gland large, indistinct, just above and posterior to tympanum; tongue pear-shaped, notched at tip, and free for half its length; inner nares large, situated laterally (width between inner nares 3.5 mm.); vocal sac openings large, half the length of jaw rami; inguinal gland large, elongate, raised above level of femur when leg is brought forward along side of body.

Relative length of fingers and toes, shortest to longest respectively, fingers 2-1-4-3, toes 1-2-5-3-4; legs relatively short; tibiotarsal articulation reaches posterior corner of tympanum; with legs folded at right angles to body the heels overlap 3 mm.; inner metatarsal tubercle about three times as large as outer; subarticular tubercles large, pointed; no tarsal fold; tips of two outer fingers tapering, narrowest at tip; large flat, median palmar tubercle seven or eight times larger than ones at bases of first and fourth fingers.

Dorsal color uniformly dark brown; obscure blackish bars on tibia, femur, and forearm; lips brownish; whitish spot on tip of snout; anterior face of femur light brown,

posterior face brown; scattered whitish subcircular spots on anterior face of knee, tibia, and tarsus; venter brownish with minute black stipulations and whitish subcircular spots.

Variation. In the type series, thirteen individuals exhibit roughly granulated venters with tips of granules whitish. One specimen has a relatively smooth venter but granules can easily be discerned under the lens. The dorsal coloration is uniform brown in most but varies to an indistinct mottling of brown and dark brown, the head is sometimes grayish. Bars on the extremities are usually brown or dark brown and obscure. The inguinal gland is dark brown marbled with white but sometimes concolor. The whitish subcircular spots on the legs are sometimes obscure. Females are not available for study. For mensural variation of adult males see Table 11.

Comparisons. Tomodactylus grandis differs from T. angustidigitorum in having a larger tympanum (56.8 per cent rather than 44 per cent of eye diameter); broad internarial width (86 per cent rather than 74 per cent of eye diameter); proportionally shorter tibia (37.7 per cent rather than 39.3 per cent of snout-vent length); larger snout-vent length (mean 27.9 mm. rather than 23.0 mm.). Differs from T. fuscus in all of the above characters and in addition tips

of digits tapering, narrowest at tip rather than conspicuously expanded and truncate. Differs from all other known members of the genus in having femur and groin concolor rather than with yellow, ochraceous, orange, or red spots; tips of fingers tapering and narrowest at tip rather than as wide as or wider than narrowest part of digit; internarial width three-fourths rather than less than one-half of eye diameter; tympanic width greater than one-half of eye diameter (56 percent rather than 50 percent or less).

Habits. The habitat of this toad seems to be the "malpais" or lava beds near Mexico City and the mountains to the south (north side of the Ajusco Mountains) to an elevation of 8,800 feet. The specimens that were captured at the type locality were found calling from lava rocks. Portions of the lava flows in this area were under agricultural use and the fields were marked off with rock fences. Numerous Temodactylus were heard calling from these fences but I was able to capture only two of them because the porous volcanic rock made their capture difficult. On one occasion several were heard calling from inside a large volcanic rock but I did not have the necessary equipment to expose them. The voice of this species is much like that of T. fuscus, a peep or whistle, but repeated more often.

Range. The known range of this species is confined to the lava beds surrounding Mexico City, up to an elevation of 8,800 feet, in the Federal District and the state of Mexico. Taylor (1940:494) collected a specimen of Tomodactylus near San Martin in the state of Mexico which he referred to angustidigitorum. I have not seen it but on the basis of geographic probability it is likely referable to T. grandis.

Locality Records. DISTRITO FEDERAL: San Pedro, 2 mi. S. Tlalpan, 7,800 ft., (TCWC 2); Tlalpan, 7,600 ft., (UIMNH 1); 4 mi. S. Villa Alvaro Obregon, 7,800 ft., (UMMZ 11).

Table 11. Analysis of individual variation of Tomodactylus grandis based on 14 adult males. Foot and tibia proportions are percentages of the snout-vent length. Tympanic proportions are percentages of the diameter of eye.

STATISTIC	S-V	FOOT		TIBIA		TYMPANUM		EYE
	mm.	mm.	%	mm.	%	mm.	%	mm.
Maximum	30.5	12.4	42.3	11.6	39.5	2.0	61.3	3.6
Minimum	25.0	10.2	38.4	9.2	33.7	1.6	53.2	2.8
Range	5.5	2.2	3.9	2.4	5.8	0.4	8.1	0.8
Mean	27.9	11.1	39.8	10.6	37.7	1.79	56.8	3.15
Standard Deviation	1.67	0.642	1.0	0.756	1.5	0.122	2.6	0.120
Standard Error of the Mean	0.447	0.181	0.26	0.202	0.40	0.033	0.69	0.028
S.E. of Standard Deviation	0.316	0.121	0.19	0.142	0.28	0.023	0.49	0.020
Variability %	6.0	5.7	2.5	7.0	4.1	6.2	4.5	3.8

DIAGNOSTIC KEY TO THE SPECIES OF TOMODACTYLUS

1. Tips of two outer fingers conspicuously expanded and truncate, one and one-half to twice the width of narrowest part of digit 2

   Tips of two outer fingers not noticeably expanded and not more than one and one-fourth times width of narrowest part of digit 4

2. Anterior and posterior faces of femur with yellowish orange, or red spots 3

   Anterior and posterior faces of femur concolor; size small (snout-vent length of males to 25 mm.); upper parts brown to dark brown; inner metatarsal tubercle nearly twice the size of outer one; femur more or less uniformly brown . . . . . Tomodactylus fuscus

3. Size large (snout-vent length to 30 mm.); upperparts mottled dark gray or dark brown; large immaculate ochraceous spots on femur; underparts usually pigmented and with whitish subcircular spots; upper lip pigmented . . . . . Tomodactylus dilatus

Size small (snout-vent length to 26 mm.); upperparts olive to olive brown; red or orange spots on femur and sometimes in groin; venter whitish with diffuse dark spotting; upper lip with whitish line . . . . . Tomodactylus albolabris

4. Tips of fingers tapering and narrowest at tip . . . 5

Tips of fingers as wide or wider than narrowest part of digit but not greatly expanded 6

5. Hand small; size small (snout-vent length to 29 mm.); upperparts pustular, concolor or mottled brownish; venter usually buff; tympanum 45 per cent of eye diameter; femur usually concolor . . . . . Tomodactylus angustidigitorum

Hand large; size large (snout-vent length to 31 mm.); upperparts pustular, indistinctly mottled brownish or grayish brown; venter grayish with diffuse dark stipulations of brown; tympanum 56 per cent of eye diameter; internarial width more than three-fourths eye diameter . . . . . Tomodactylus grandis

6. Legs long, tibiotarsal articulation reaches beyond arm insertion when brought forward along side of body 7

Legs short, tibiotarsal articulation does not reach arm insertion when leg brought forward along side of body; when folded at right angles to main axis of body heels do not overlap; dorsum grayish, mottled or spotty; venter grayish, usually without spots; voice a "bleat" rather than a peep or whistle . . . . . Tomodactylus orarius

7. Femoral spots yellow; tips of fingers expanded; upperparts pustular, mottled greenish or brownish; venter whitish, occasionally with scattered brown spots. Tympanic width less than one-half of eye diameter (45 per cent) . . Tomodactylus n. nitidus

Femoral spots yellowish orange or orange; upperparts somewhat pustular, mottled greenish brown or chocolate brown; venter whitish with frequent dark brown or black spotting; tips of fingers expanded and truncate; tympanic width one-half eye diameter (50 per cent) . . . . . .Tomodactylus n. petersi

DISCUSSION OF SPECIFIC RELATIONSHIPS

The seven species and two subspecies of Tomodactylus segregate into four distinct groups on the basis of (1) color pattern; (2) color; (3) general body shape; (4) geographic range. There is a varying amount of overlap in the distribution of two of these groups but there is no indication of intergradation.

The first group is comprised of three species, T. angustidigitorum, T. fuscus, and T. grandis, which are distinctly similar with respect to color pattern, color, body shape, and geographic range. Their general dorsal color is uniform brown. Occasionally, an indistinct mottling of brown and dark brown may be present. A distinct or obscure loreal stripe is always present and the barring of the arms and legs is obscure. The ventral pattern varies considerably in the amount of pigmentation and the number of spots but it generally is the same color in all three species. The general body shape is robust with somewhat slender arms and legs. The snout is round or blunt. The tips of the fingers are tapering and narrowest at the tips in angustidigitorum and grandis but conspicuously expanded and truncate in fuscus.

All three species are found along the southern edge of the Mexican Plateau in the Pine-oak Forest between elevations

of 5,000 to 8,800 feet. T. grandis and T. fuscus inhabit opposite sides of the same mountain range, separated from each other by the higher elevations along the crests. This altitudinal barrier is probably due to the temperature tolerances of both species. Neither species has been observed above 8,800 feet nor below 7,500 feet. The range of T. fuscus extends farther to the west than that of T. grandis, but it probably does not meet the range of T. angustidigitorum (see Map 4).

The second group is comprised of two species, T. orarius and T. nitidus. The latter has two geographic races, T. nitidus nitidus and T. nitidus petersi. This group has the largest geographic range of the genus. The group inhabits several vegetation types: Pine-oak Forest, Tropical Deciduous Forest, Thorn Forest and Arid Tropical Scrub. Its range includes all of south-central Mexico and portions of the Pacific slopes and coastline as far north as the states of Sinaloa and Durango. These toads range altitudinally from sea level to 8,000 feet in the mountains. Intergradation between the geographic races of nitidus is to be expected in the western part of the Balsas Basin. T. orarius is known only from the Pacific coastal regions of Nayarit, Colima, and Michoacan below 1,500 feet, and its range is not known to overlap with that of nitidus.

The dorsal color pattern of both species is mottled with the ground color varying from light gray to chocolate brown. The darker coloration overlying the ground color varies from tan or grayish green to black. The ventral patterns are similar, varying from dirty gray to white, but one geographic race, T. n. petersi, differs in the extent of ventral spotting. The bars of the arms and legs are distinct in the two species but occasionally they are obscure in orarius. Nevertheless, the barring of the limbs of the nitidus group is much more distinct than that found in the angustidigitorum group. A distinct interorbital bar and loreal stripe are present in both species. The femoral and groin spots vary from yellowish white to orange.

The body shape is robust with relatively strong arms and legs. The tips of the two outer fingers are as wide or wider than the narrowest part of the finger. There is a considerable amount of individual variation of the digital expansion but, generally, the tip does not exceed one and a fourth times that of the narrowest part of the digit.

The third and fourth groups are comprised of a single species each. Both are distantly related to the nitidus group. T. dilatus, the third group, and T. albolabris, the fourth group, are restricted in their geographic range. Both occur in the northwestern end of the Sierra Madre

del Sur. T. dilatus is found in the pine-oak forest between elevations of 7,500 to 8,000 feet, and is known from only two localities in Guerrero - Omiltemi, and the mountains west of Mazatlan. These localities are about 20 miles apart in the same mountain range.

T. albolabris is found in the pine-oak and tropical deciduous forests between elevations of 2,700 and 4,000 feet. Its known range is restricted to three localities, all of which are within seven or eight miles of each other and in the same valley.

Both groups show an affinity to the nitidus group in the presence of femoral and groin spots. The only other similarity is the distinct dorsal color pattern of mottling in dilatus and the pattern of indistinct mottling in albolabris. T. dilatus has a large robust body with the tips of the two outer fingers conspicuously expanded and truncate; the canthus is sharply angled and the tympanum very small; the dorsum is roughly pustular, brownish, and mottled with black. The femoral and groin spots are ochraceous in color. The venter is heavily granular, whitish to grayish brown with white subcircular spots.

T. albolabris has a small slender body with relatively long legs and slender arms. The snout is pointed and the tympanum small, but larger than that of dilatus. The tips

of the two outer fingers are conspicuously expanded and truncate. The dorsal color pattern may be uniform olive to reddish brown in color, or indistinctly mottled with olive and brown. The ventral surface is white with diffuse dark brown spotting.

There seems to be no correlation between vegetation or any other aspect of the habitat and digital expansion in any of the groups. T. angustidigitorum, with its tapering digits, climbs shrubs and trees with ease. T. fuscus, with its expanded digits, may be found sitting on rocks. I assume that those species in which digital expansion occurs, are better climbers and can climb to greater heights than those that lack the expansions.

A total comparison of mensural relationships between the various forms of Tomodactylus is found in Figures 6 through 9; see also Table 12.

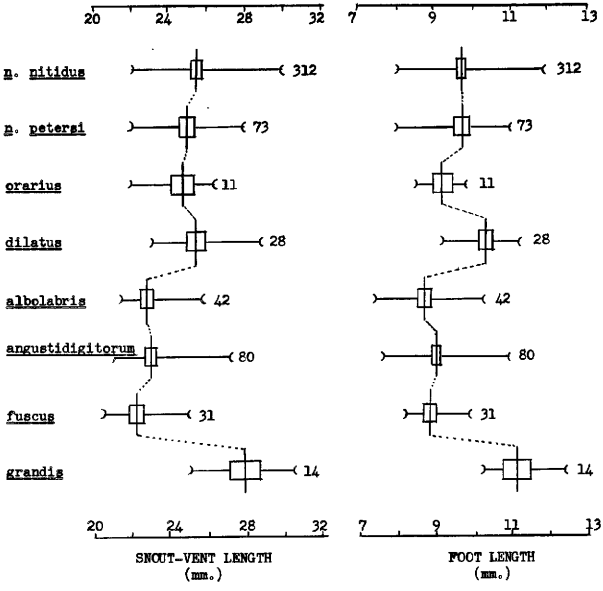


Fig. 6. Variation in the length of the snout-vent and foot of the species and subspecies of Tomodactylus. Dotted lines connect the means; vertical line represents the mean, open rectangle twice the standard error, horizontal line the range in variation. The number to the right of the horizontal line is the number of specimens used in the analysis.

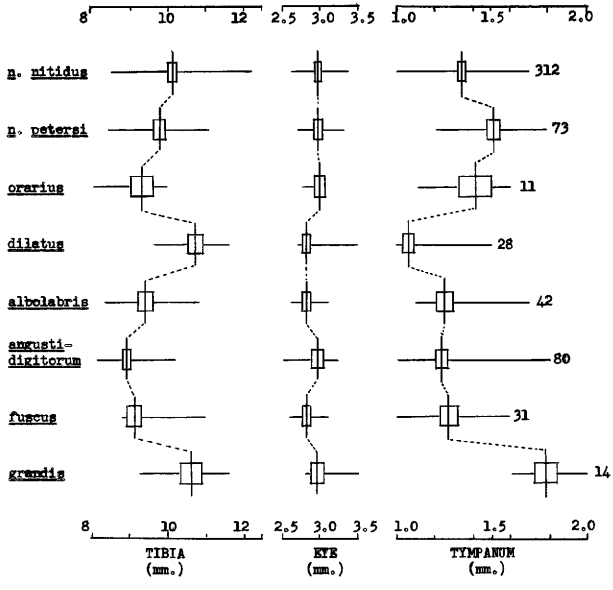
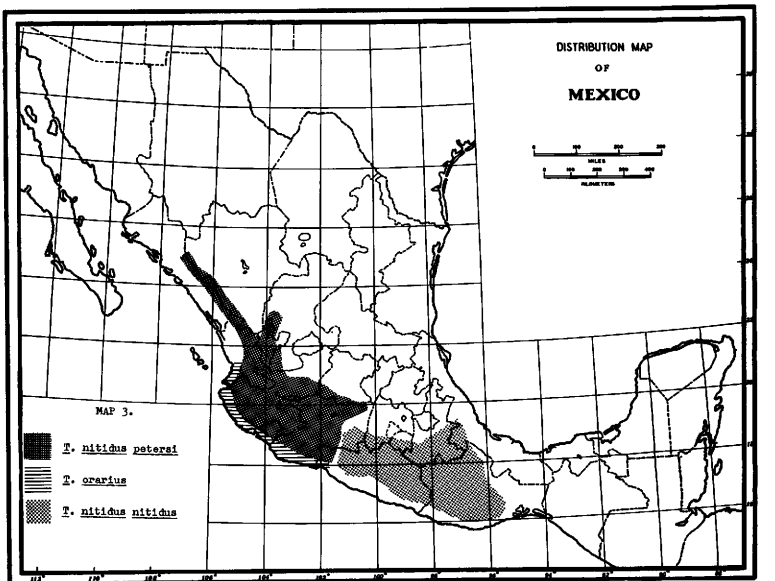
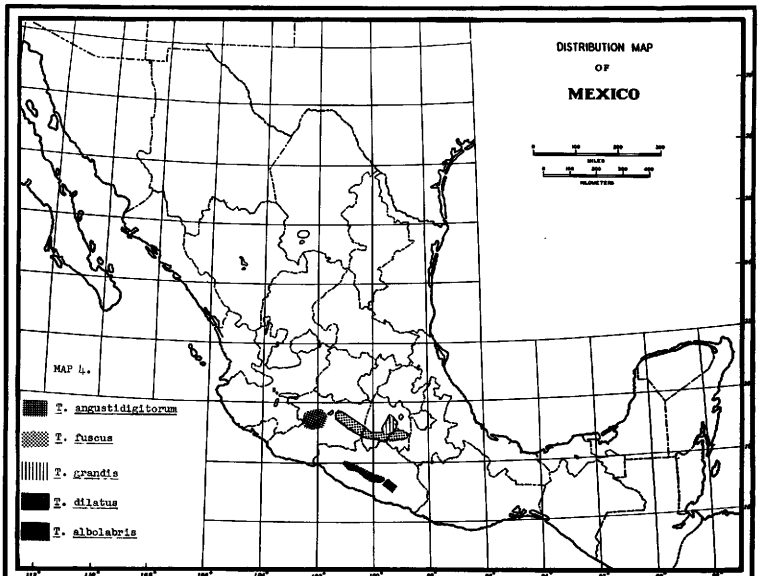


Fig. 7. Variation in the length of the tibia and in the width of the eye and tympanum of the forms of Tomodactylus. Dotted lines connect the means; vertical line represents the mean, open rectangle twice the standard error, horizontal line the range in variation. The number to the right of the horizontal line is the number of specimens used in the analysis.


DISTRIBUTION MAP
OF
MEXICO
MAP 3.
T. nitidus peterai
T. orarius
T. nitidus nitidus


DISTRIBUTION MAP
OF
MEXICO
MAP 4.
T. angustidigitorum
T. fuscus
T. grandis
T. dilatus
T. albolabris

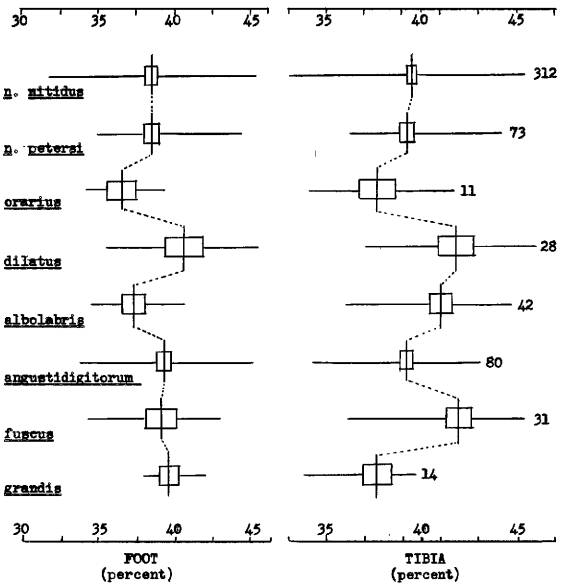


Fig. 8. Variation in the proportions of the length of the foot and tibia of the species and subspecies of Temodactylus. Figures for proportions are percentages of the snout-vent length. Dotted lines connect the means; vertical line represents the mean, open rectangle twice the standard error, horizontal line the range in variation. The number to the right of the horizontal line is the number of specimens used in the analysis.

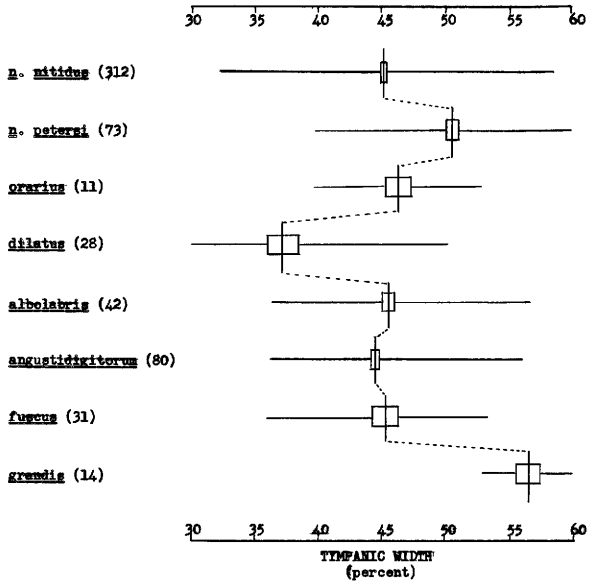
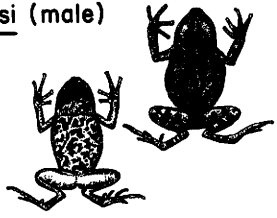


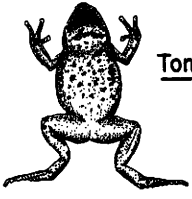
Fig. 9. Variation in the proportion of the tympanic width of the forms of Tomodactylus. Figures for the proportions are percentages of the eye diameter. Dotted line connects the mean; vertical line represents the mean, open rectangle twice the standard error, horizontal line the range in variation. The number to the right of the species name is the number of specimens used in the analysis.

Table 12. Proportional measurements of the adult males of the species and subspecies of Teredactylus. The foot and tibia lengths are percentages of the snout-vent length. The tympanic widths are percentages of the eye diameter.

STATISTIC	nitidus nitidus	nitidus petersi	orarius	dilatus	albolabris	angustidigitorum	fuscus	grandis
No. in Sample	312	73	11	28	42	80	31	14
FOOT (%)								
Maximum	45.4	44.2	39.6	47.0	42.5	46.5	43.8	52.3
Minimum	32.7	35.2	34.6	36.4	34.0	33.3	34.3	38.4
Mean	38.5	38.9	37.3	40.5	37.9	39.4	39.3	39.8
S.D.	0.8	1.8	1.4	3.1	2.1	2.1	2.2	1.0
TIBIA (%)								
Maximum	45.6	44.2	40.9	47.4	44.8	43.1	45.7	39.5
Minimum	32.7	36.1	34.8	36.9	36.2	34.2	36.0	33.7
Mean	39.6	39.3	37.8	41.9	41.1	39.2	41.9	37.7
S.D.	0.9	1.8	1.7	2.9	2.1	1.4	2.0	1.5
TYMPANUM (%)								
Maximum	58.0	60.0	53.3	50.0	56.0	56.0	53.3	61.3
Minimum	33.3	40.0	40.0	30.0	36.6	36.6	36.0	53.2
Mean	45.8	50.6	46.9	37.6	45.8	44.3	45.5	56.8
S.D.	1.4	3.1	4.3	4.9	2.2	4.5	3.8	2.6

Tomodactylus nitidus petersi (male)

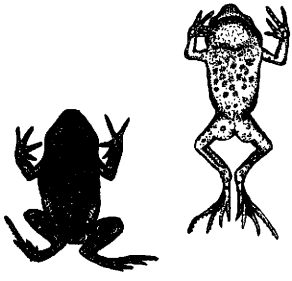




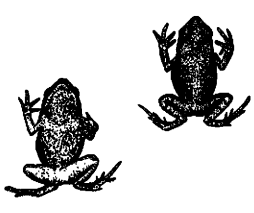
Tomodactylus nitidus nitidus (male)

T. orarius (Type)

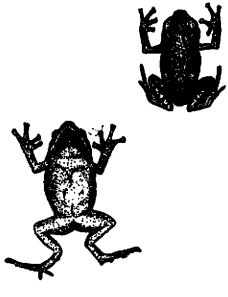
Figure 10.



Tomodactylus grandis (male)



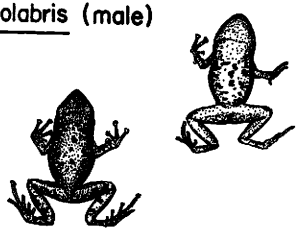
T. angustidigitorum (male)



T. fuscus (male)

Figure 11.

T. albolabris (male)



T. dilatus (male)

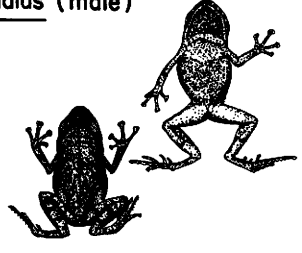


Figure 12.

SUMMARY

Toads of the genus Tomodactylus occupy five major vegetative types and seven physiographic provinces along the edges of the Mexican Plateau, in the Balsas Basin, and in the Sierra Madre del Sur in southern Mexico. The known range extends from eastern Sinaloa on the west and central Veracruz on the east southward nearly to the Isthmus of Tehuantepec and altitudinally from near sea level, as in Nayarit, to well over 8,000 feet in the Ajusco Mountains south of Mexico city. Apparently the animals do not occur below 3,000 feet on the eastern slopes of the Sierra Madre del Oriental.

Correlated with diversified topography, climate, and vegetation, members of the genus exhibit considerable geographic variation. Tomodactylus nitidus is the most wide ranging species and occupies the main mountain masses between elevations of 1,500 and 7,800 feet. The species is comprised of two well marked subspecies, T. n. nitidus and T. n. petersi. Two species, T. angustidigitorum and T. fuscus, occupy the higher parts of the transverse volcanic region, mainly the upper slopes of the Ajusco Mountains. Two others, T. dilatus and T. albolabris occur in the isolated Sierra Madre del Sur, the former at high elevations in the

Pine-fir Forest, the latter at low elevations in the Pine-oak and Tropical Deciduous forests. The coastal lowlands of Sinalea, Nayarit, Colima, Jalisco, and Michoacan are inhabited by a distinct species, T. *erarius*, as are the lava beds along the southern edge of Mexico City, T. *grandis*, both of which are herein described for the first time.

The analyses of the specific relationships of the genus indicated that on the bases of color, color pattern, body shape, and geographic range the species form four natural groups - the *angustidigitorum* group, which includes T. *fuscus*, T. *grandis*, and T. *angustidigitorum*; the *nitidus* group, which includes T. *n. nitidus*, T. *n. petersi*, and T. *erarius*; the *dilatus* group and the *albolabris* group, each of which is comprised of a single species.

The large species described by Taylor as T. *macrotympanum*, from the Pine-oak Forests of northern Hidalgo, is transferred to the genus *Syrrhophus*.

LITERATURE CITED

Davis, W. B., and J. R. Dixon. 1955. Notes on the Mexican toads of the genus Tomodactylus with the descriptions of two new species. Herpetologica, 11:154-160.

Duellman, W. E. 1954. The amphibians and reptiles of Jorullo Volcano, Michoacan, Mexico. Occas. Papers Mus. Zool. Univ. Michigan, no. 560:1-24.

Firschein, I. L. 1954. Definition of some little-understood members of the leptodactylid genus Syrrhophus, with a description of a new species. Copeia, (1):48-58.

Gadow, H. 1910. The effect of altitude upon the distribution of Mexican amphibians and reptiles. Zool. Jahrb. Jena. Abt. F. Syst. 29:689-714.

Goldman, E. A. 1951. Biological investigations in Mexico. Smithsonian Misc. Coll., 115(4017):1-476, 70 pls., 1 map.

Goldman, E. A. and R. T. Moore. 1945. The biotic provinces of Mexico. Jour. Mamm., 26(4):346-360.

Gunther, A. C. L. G. 1900. Biologia Centrali-Americana, Reptilia and Batrachia. pp. 219-220.

Hill, R. T. 1908. Growth and decay of the Mexican Plateau. Eng. and Mng. Jour., 85(14):681-688.

Leopold, A. S. 1950. Vegetation zones in Mexico. Ecology, 31(4):507-518.

Martin del Campo, R. 1940. Una observacion del desarrollo de Tomodactylus nitidus. An. Inst. Biol., 11(2): 745-746.

Mayr, E. 1942. Systematics and origin of species. vii-334, New York, Columbia University Press.

Mayr, E., E. G. Linsley, and R. L. Usinger 1953. Methods and principles of systematic zoology. v+328, New York, McGraw-Hill Book Co., Inc.

Ordonez, E. 1936. Principal physiographical provinces of Mexico. Bull. Amer. Assoc. Petr. Geol., 20(10): 1277-1307.

Parker, H. W. 1927. A revision of the frogs of the genera Pseudopaludicola, Physalaemus, and Pleuroderma. Ann. and Mag. Nat. Hist., 20(118):450-478.

Peters, W. 1869. Eine Mittheilung uber mexicanische Amphibien, welche Hr. Berkenbusch in Puebla auf Veranlassung des Hrn. Legationsrathe von Schlozer dem zoologischen Museum zugesandt hat. Monatab. Akad. Wiss. Berlin, pp. 874-881.

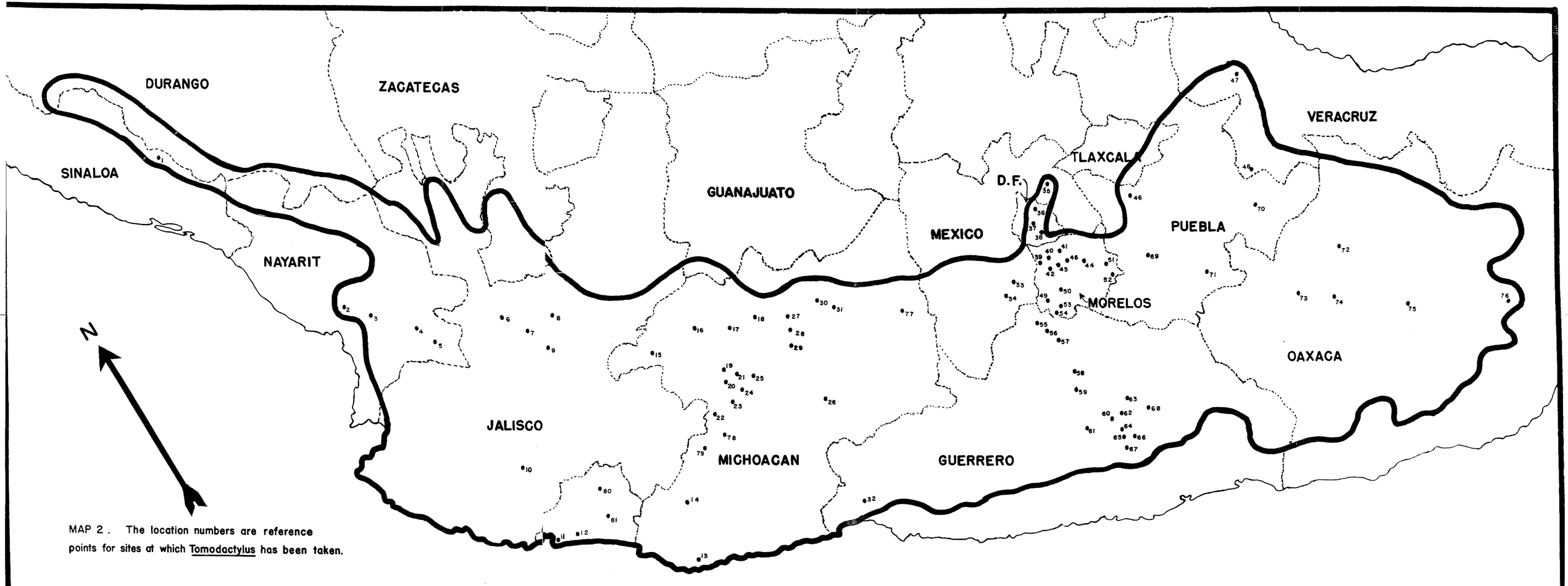
Schmidt, K. P., and F. A. Shannon 1947. Notes on amphibians and reptiles of Michoacan, Mexico. Fieldiana:Zool. (Chicago Nat. Hist. Mus.) 31(9):68-69.

Smith, H. M. 1949. Herpetogeny in Mexico and Guatemala. Ann. Assoc. Amer. Geol., 39(3):219-238.

Taylor, E. H. 1940. Herpetological miscellany. Univ. Kan. Sci. Bull., 26(15):489-560.

_____. 1943. Herpetological novelties from Mexico. Univ. Kan. Sci. Bull., 29(2):343-361.

Thayer, W. N. 1916. The physiography of Mexico. Jour. Geol., 24:61-94.



MAP 2. The location numbers are reference points for sites at which Tomodactylus has been taken.