A REVIEW OF THE LIZARDS OF THE IGUANID GENUS TROPIDURUS IN PERU

By James R. Dixon and John W. Wright
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A REVIEW OF THE LIZARDS OF THE IGUANID GENUS *TROPIDURUS* IN PERU

By James R. Dixon and John W. Wright

Abstract: Eight species of the genus *Tropidurus* are known to occur in Peru, representing two major species groups, occipitalis and peruvianus. The *occipitalis* group, containing *occipitalis*, *koepckeorum*, and *stolzmanni*, is characterized by having keeled, mucronate, imbricate dorsolateral scales and by having a prominent mid-dorsal crest. Members of this group are primarily scansorial. The *peruvianus* group, containing *peruvianus*, *melanopleurus*, *theresiae*, *thoracicus* and *tigris*, is characterized by having granular, juxtaposed, smooth dorsolateral scales. Members of this group are largely ground dwellers. Species within each group differ most conspicuously from other members in body size, color, and color pattern. All species except *thoracicus* have marked sexual dimorphism in size, color, and color pattern. *Tropidurus peruvianus* consists of several described races, two of which occur in Peru: *p. peruvianus* and *p. satinicola*. We present descriptions for three proposed races of *thoracicus*, *t. thoracicus*, *t. talarae* new subspecies, and *t. icae* new subspecies. All other species are considered monotypic.

With the exception of *stolzmanni*, all species in Peru are restricted to xeric coastal habitats. *Tropidurus stolzmanni* occurs in the dry interandean Amazonian valleys of northern Peru. Three species (*peruvianus*, *occipitalis*, and *thoracicus*) have extensive geographic ranges on the coastal plain. *Tropidurus peruvianus* essentially is intertidal and independent of terrestrial vegetation, whereas *thoracicus* and *occipitalis* occur in vegetated areas. *Tropidurus koepckeorum* and *tigris* occur in the rocky habitats of coastal hills and Andean foothills. *Tropidurus theresiae* has a limited distribution in essentially intertidal habitats. All of the coastal species occur in limited sympatry with one to three species. Only three Peruvian species have geographic ranges that extend beyond Peru, *peruvianus* (Chile and Ecuador), *occipitalis* (Ecuador), and *melanopleurus* (Bolivia).

Introduction

The most recent review of the lizards of the genus *Tropidurus* in Peru was prepared by Mertens (1956), in which he reviewed known populations and types and recognized five species (*holotropis*, *occipitalis*, *peruvianus*, *theresiae*, *thoracicus*). He also recognized three races of *T. occipitalis* (*occipitalis*, *koepckeorum*, *stolzmanni*) and three of *T. peruvianus* (*peruvianus*, *salinicola*, *tigris*). Subsequently, Etheridge (1970b) demonstrated *Tropidurus holotropis* to be a synonym of *Plica umbra*.

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During November and December of 1968, we had the opportunity to study populations of *Tropidurus* over a wide geographic area in Peru while conducting other investigations. Our studies centered around observations of the habits, habitats, and color and color patterns of these lizards. These have enabled us to form a more accurate estimate of the relationships of the various populations of *Tropidurus* in Peru. We propose herein that seven of the eight populations recognized by Mertens (1956) be accorded specific rank. The status of the eighth population, *salinicola*, is discussed, but conclusions regarding its allocation are deferred pending additional studies. Also, we propose the recognition of three races of *Tropidurus thoracicus* (*t. thoracicus*, *t. icae* new subspecies, *t. talarae* new subspecies).

Subsequent to our work in Peru and after this manuscript was written, we examined a specimen of *T. melanopleurus* from Morro Sana, 65 km W Tacna, Departo. Tacna (MVZ 99637). Etheridge (personal communication) informed us that he is aware of additional specimens from Peru that are to be reported by him in a general treatment of the species. We have included *melanopleurus* in the introductory statements and key, but provide no additional discussion or description of this species.

**Disposition of Specimens Examined**

Most of the specimens (approx 700) used in this study are in the Herpetological collections of the Natural History Museum of Los Angeles County (LACM) or Texas Cooperative Wildlife Collections (TCWC) of Texas A and M University. Additional specimens cited are in the following collections: American Museum of Natural History (AMNH); British Museum (Natural History), (BMNH); Louisiana State University, Museum of Zoology (LSUMZ); Musee National d’Histoire Naturelle, Paris (MNHN); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Naturhistorisches Museum, Wien (NMW); National Museum of Natural History (USNM); and Zoologisches Museum, Berlin (ZMB).

**TROPIDURUS** Wied


Species of the genus *Tropidurus* west of the continental divide in South America can be grouped into two apparently natural groups: (1) the *peruvianus* group (*peruvianus*, *melanopleurus*, *theresiae*, *thoracicus*, *tigris*, and two extralimital species in Chile) characterized by having smooth, juxtaposed, granular dorsal scales and weakly developed mid-dorsal row of scales and (2) the *occipitalis* group (*koepckeorum*, *occipitalis*, *stolzmanni*, and several (7±) extralimital species occurring on the Galapagos Islands) characterized by having keeled, imbricate dorsal scales and the mid-dorsal row of scales enlarged to form a crest of spines. Members of the *peruvianus* group are terrestrial, occurring on sandy beaches, sand dunes, and on small rocks and boulders; whereas members of the
occipitalis group (in Peru) are scansorial, occurring on trees, bushes, boulders, piles of debris, and fences. The following species accounts and discussions are arranged with respect to these two groups.

**Key to the Species of Tropidurus of Peru**

1a. Dorsolateral scales keeled and imbricate (occipitalis group) .................. 2
1b. Dorsolateral scales smooth and granular (peruvianus group) ................ 4
2a. Chin and gular region of both sexes with rows of dark spots, more distinct in males; scales around midbody 66 to 77 ........................................koepckeorum
2b. Chin and gular region unmarked, mottled or with stripes .................. 3
3a. Distinct dark spot (usually black) on posterior margin of interparietal scale; no stripes in gular region; scales around midbody less than 60 ....occipitalis
3b. Interparietal scale unspotted; gular region with stripes, more distinct in males; scales around midbody more than 80 .............................stolzmanni
4a. Median row of dorsal scales enlarged, sometimes keeled, forming a continuous row; no greenish blue spot on throat or red eye ring in either sex .. 5
4b. Median row of dorsal scales not enlarged or keeled; a greenish blue spot on throat and a red eye ring present in males; white throat and dull red eye ring in females ........................................................................theresiae
5a. One row of scales between nasal scale and first supralabial; chin black or with distinct black spots or chevrons in males, unmarked or with diffuse bars or spots in females .......................................................... 6
5b. Two or more rows of scales between nasal scale and first supralabial; chin white or with diffuse gray stripes or bands in both sexes ..............thoracicus
6a. Lateral body scales small, granular, and juxtaposed, grading abruptly into much larger ventrals ................................................................. 7
6b. Lateral body scales small and imbricate, grading smoothly into subequal ventrals .................................................................melanopleurus
7a. Gular area with distinct black spots in males, diffuse crossbars or spots in females; brachial scales strongly keeled with free projecting spines; brachial scales subequal to nostril diameter ......................................tigris
7b. Gular area with distinct black chevrons in males, unmarked in females; brachial scales weakly keeled without free projecting spines; brachial scales about half the size of nostril diameter ..............................peruvianus

**Tropidurus peruvianus Group**

**Tropidurus peruvianus** (Lesson) 

Stellio peruvianus Lesson 1826. Voy. Coquille, Reptiles, plate 2, fig. 2.


*More complete synonymies for this and other species discussed herein can be found in Mertens (1956) and Etheridge (1970a).*
Figure 1. Dorsal view of representative adult male specimens of species of the Tropidurus peruvianus group in Peru. Bottom to top: T. peruvianus—LACM 49046, 116 mm S-VL; T. theresiæ—LACM 49065, 69 mm S-VL; T. thoracicus—LACM 48929, 82 mm S-VL; and T. tigris—LACM 48839, 89 mm S-VL.
Figure 2. Ventral view of representative adult male specimens of species of the *Tropidurus peruvianus* group in Peru (specimens and order are same as in Figure 1).
Holotype: MNHN 6873. Type locality: Sea coast at Callao and Paita, Peru (restricted to Callao, Departo. Lima, Peru, by Mertens 1956).

Diagnostic characters. Tropidurus peruvianus is distinguished from members of the occipitalis group by having small, granular dorsolateral scales, rather than large, keeled and imbricate dorsolateral scales. Within the peruvianus group, peruvianus is distinguished from thoracicus by the presence of one row of scales between the nostril scale and the first labial and bold black chevrons on the throat in males, rather than two or more rows of scales between the nasal scale and the first labial and no distinct black chevrons on the throat of males; from theresiae by the presence of an enlarged vertebral row of scales and the absence of an orange-red eye ring; from tigris by having distinct black throat chevrons in males and small scales on the upper arm without free projecting spines, rather than distinct black, transverse rows of spots on the throat of males and large scales on the upper arm with free projecting spines at the posterior tip.

Variation. At the present time there are two recognized races of this species in Peru (Mertens 1956) and six in Chile (Donoso-Barros 1966). Populations of T. peruvianus in southern Peru are poorly represented in collections, and as we have no firsthand experience with these populations, the following analysis is largely restricted to a discussion of populations occurring north of Ica.

Available samples of peruvianus can be grouped into three larger morpho-geographical samples: a northern sample (T. peruvianus subspecies), representing populations occurring along the coast from the Sechura Desert north to Tumbes; a central sample, referable to T. p. salinicola, representing populations from Huacho area north to the vicinity of Pativilca; and a southern sample, T. p. peruvianus, representing populations from Callao to the Paracas Peninsula.

The range and mean snout-vent length of adult males in the northern sample is 93 to 98 (96.3) mm, adult females 68 to 78 (75.2) mm; in the p. salinicola sample, adult males 51 to 72 (62.3), adult females 50 to 64 (57.1); and in p. peruvianus, adult males 90 to 103 (98.3), adult females 78 to 97 (84.6). The range and mean number of scales around the body are: northern sample, 127 to 153 (138.3); salinicola, 121 to 135 (127.2); and peruvianus, 116 to 147 (135.9). Range and mean number of scales in the dorsal row from occiput to rump are: northern sample, 78 to 99 (87.6); salinicola, 72 to 85 (80.2); peruvianus, 78 to 91 (83.1).

Specimens in all samples share many aspects of color and color pattern. The color pattern of males ranges from a dorsal ground color of olive-tan to greenish olive with a wide vertebral stripe of yellowish cream (Fig. 1). Overlying the ground color are eight to 10 pairs of thin, black transverse lines, separated along the median line by the yellowish cream vertebral band; entire dorsal surface of body and limbs profusely spotted with small dots of yellowish cream, forelimbs banded with narrow black lines on ground color; top of head brown; side of head with a pair of thin, black stripes from below eye to cheek, and from eye to nape; black chevron marks of throat reach labials and lower side of head (Fig. 2), forming a series of crescent-shaped black marks when viewed from the side of head; venter white in juveniles; subadult males have some black suffusion in chest and groin regions with yellow tint on remainder of venter; adult males with bright
orange-red to yellowish orange color on venter and mixed with black of chest, throat, and groin, and between black chevrons of chin.

Females range in ground color from a yellowish tan to a greenish olive or blue-gray, with the vertebral area slightly lighter in color, but not as bold as in males (Fig. 3). Females tend to have pale white vents with some indication of black chevrons on the throat (Fig. 4). A wide black to reddish brown stripe is present along the side of the body from neck to groin in young, juveniles and sub-adults. This color generally fades to ground color in adult females, with only a small patch of color left in the groin. Both juvenile males and females have a bright golden yellow spot in the groin that disappears in maturing males, and turns reddish brown in maturing females.

The northern sample has a much lighter venter and conversely, a more bold pattern of chevrons on the throat than individuals in the sample of *p. peruvianus*. Male specimens of the latter are almost melanistic, with considerable amounts of black on the throat, chest, groin, and along the anterioventral surfaces of the arm. The melanism tends to obscure the throat chevrons and to enhance the brightness of the orange and yellows. Specimens in the *p. salinicola* sample are somewhat intermediate in color pattern between the other samples, with dorsal and ventral patterns less distinct. The *salinicola* sample also contains individuals with the smallest adult size. The northern and southern populations appear to be more similar in such characters as scales around the body, snout-vent size, and number of scales in the dorsal crest, whereas *salinicola* seems to differ in all of these characters (Fig. 5).

**Habitat and natural history.** *Tropidurus peruvianus* is found throughout the immediate coastal region of Peru, inhabiting rock cliffs, bluffs, outcrops, mud cliffs, salt crust beaches, sand dunes, and sand flats, with or without vegetation (Fig. 6). As far as we have been able to determine, *peruvianus* is restricted to the coastal habitats, extending inland one or two km from the tidal zone. Most individuals observed by us were found within 100 m of the water.

An examination of stomachs of individuals taken from the Paracas area indicated the lizards were feeding on sand fleas, cockroaches, beetles, ants, and flies.

All adult females taken in July, August, September, November, and December contained yolked ovarian follicles and oviducal eggs, suggesting a long reproductive season. The clutch sizes of northern sample are 3 to 5 (4.1) eggs, *salinicola*, 2 to 3 (2.3) eggs, and *peruvianus*, 2 to 5 (3.5) eggs.

**Comments.** There is little doubt that the population named by Mertens (1956) as *salinicola* is closely related to *peruvianus*, but there is some question as to whether or not the two are conspecific. The differences in color, color pattern, and scutellation are subtle, but the differences in body size are such that they may well reflect a barrier to gene flow. We prefer to maintain *salinicola* as a race of *peruvianus* until such time as information becomes available for populations from the approximately 100 km geographical “gap” between the two.

**Distribution.** *Tropidurus peruvianus* is the widest ranging coastal species of the genus, occurring from southwestern coastal Ecuador, south to northern
Figure 3. Dorsal view of representative adult female specimens of species of the *Tropidurus peruvianus* group in Peru. Bottom to top: *T. peruvianus*—LACM 49040, 93 mm S-VL; *T. thersites*—LACM 49071, 44 mm S-VL; *T. thoracicus*—LACM 49001, 72 mm S-VL; and *T. tigris*—LACM 48838, 68 mm S-VL.
Figure 4. Ventral view of representative adult female specimens of species of the *Tropidurus* *peruvianus* group in Peru (specimens and order are same as in Figure 3).
Figure 5. Dorsal (bottom) and ventral (top) views of adult male specimens of *Tropidurus peruvianus*, illustrating the marked size difference between populations. Specimen at left (dorsal and ventral, LACM 49018, 112 mm S-VL) collected at 12 km S and W (by rd) Paracas, and specimen at right (LACM 49021, 66 mm S-VL) collected at 24.7 km N (by rd) Pativilca.
Figure 6. Outline maps of the coastal area of Peru showing localities for specimens of the genus Tropidurus: A - *T. peruvianus* (○); B - *T. t. thoracicus* (♦), *T. t. talarae* new subsp. (▲), and *T. t. icae* new subsp. (▽); C - *T. theresiae* (●) and *T. tigris* (□); D - *T. koepckeorum* (♦); E - *T. occipitalis* (■) and *T. stolzmanni* (▼). See Distribution sections for localities.
Chile, an airline distance of some 3,600 kilometers. The range in elevation is from sea level to approximately 200 m. A total of 208 specimens have been examined from Peru.

No specific locality, USNM 5704, 5762 (2). **Tumbes.** 1.2 km S Cancas, TCWC 28644. **Piura.** Bayovar, MVZ 82340, 82342-43; 2 km NE Bayovar, MVZ 84706; 3.7 km ENE Organos, LACM 49035, TCWC 28642-43; Paita, USNM 73367-68; Reventazon, MVZ 82383; 35 km SSE Sechura, MVZ 82337-39, 82379-82; 4 km N Talara, MVZ 82386; Tric Trac, MVZ 82385, 82341, 84705, 85364-78; Lobitos Dist., BMNH 1926.3.24.22-27. **Lambayeque.** Isla Lobos de Tierra, USNM 38560; mouth of Rio Sana, MVZ 119266-67, 119272-76, 119278-79. **Libertad.** 20 km N Chimbote, TCWC 28461. **Ancash.** 159 km S Casma, MVZ 82344, 82378; 2 km N Culebras, TCWC 28645-46; 41 km SE Huarmey, RT 53-54 (in LSUMZ); 44 km N Huarmey, RT 357 (in LSUMZ); 64 km SSE Huarmey, RT 55-67 (in LSUMZ); 12 km N, 1 km W Pativilca, LACM 40922-34, TCWC 28627-40; 24.7 km N Pativilca (km 213), LACM 49021, 39.7 km NNE Pativilca, LACM 49036-37. **Lima.** Ancon, USNM 13980; near Callao, USNM 68735; 2 km NW Cerro Azul, LACM 49052-58, TCWC 28658-59; Cerro Azul, LACM 49051, TCWC 28626, 28653-57; Choisca Canyon, USNM 51514-16; Cruz de Hueso, USNM 75391; 13 km S, 7 km W Huacho, LACM 49020, 49038, TCWC 28650-51; Isla Chincha Norte, USNM 38561-68; Isla San Lorenzo, LACM 9342-46, USNM 17538-40; 3 km NW San Antonio, LACM 49059, TCWC 28660-61; Callao, BMNH 1900.6.20.1. **Ica.** Isla Vieja, USNM 96019, 166478 (13); 5 km SSW Paracas, MVZ 119268-71, 119277, 119280-81; 7.2 km S and W of Paracas, LACM 49048-50, TCWC 28620-25; 17 km S and W of Paracas, LACM 49043-47, 49016-19, TCWC 28610-19; 12 km S and W of Paracas, LACM 49039-42; near Pisco, USNM 52210; Pto. San Juan (Marcona), LACM 9347; Isla Chincha, LACM 5866. **Arequipa.** Mollendo, AMNH 38034-35, CASES 6606, USNM 13825; Punta de Lobos, MVZ 57808.

Literature locality records are: **Tumbes.** Between Bocapan and Penas Redondas (Mertens 1956). **Piura.** South of Mancora (Mertens 1956); Negritos (Burt and Myers 1942). **Libertad.** Jequetepeque Valley (Cope 1876); Pacasmayo (Mertens 1956). **Lima.** Chancay, Chicla, Laguna de Villa, La Herradura, La Ventanilla (Mertens 1956); Puerto Salinas, Pucusana (Mertens 1956); Surco (Burt and Burt 1930). **Ancash.** Near Puerto Casma, Isla Tortugas (Mertens 1956).

**TROPIDURUS THERESIAE** STEINDACHNER


**Holotype:** Lost?1 Type locality: Ancon, Peru.

**Diagnostic characters:** *Tropidurus heresiae* is a member of the *peruvianus* group differing from *peruvianus, tigris* and *thoracicus* by having a greenish blue or blue-black throat spot and an orange-red eye ring in adult males, and no enlarged keeled vertebral row of scales.

**Variation.** We have examined two samples representing the northern and southern populations. No adequate series of specimens is available from the middle of the known distribution.

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1Mertens (1956) reported that the holotype was in NMW. Dr. Franz Tiedemann, in charge of the Zoologische Abteilung, informed us (personal communication) that the specimen was never deposited in NMW. Thus, the disposition of the specimen is unknown. Fortunately, the description of the specimen and the illustration presented by Steindachner (1902, taf. 1, fig. 2) are sufficient to establish identity between the holotype and the species discussed here.
Figure 7. Dorsal view of ontogenetic series of *Tropidurus thersiae*, illustrating change in color pattern. Size (S-VL) from bottom to top: 37 mm (LACM 49062, juv.), 44 mm (LACM 49063, juv.), 55 mm (LACM 49068, female), 66 mm (LACM 49079, female).
The northern sample, taken from Punta El Paraiso, has 132 to 154 (141.5) scales around the body (SAB). The southern sample, from the Paracas Peninsula, some 380 airline kilometers to the south, has 147 to 161 (153.8) SAB. One specimen from 120 kilometers north of the Paracas Peninsula has 150 SAB. Based on these data, the number of scales around the body appears to increase from north to south.

There is a striking amount of ontogenetic change in color and pattern from juvenile to adult in this species (Fig. 7). The dorsal ground color of juveniles is tan to yellowish tan, with a broad lateral black band with undulating edges, from neck to tail; a dorsolateral black band with undulating edges from nape to groin; a series of paravertebral black spots from nape to tail. The dorsal surface of limbs tan, with scattered irregular black spots. The posterior edge of thigh has an undulating black band from knee to tail; dorsal surface of head usually unmarked, tan or reddish tan; chin, throat, chest and venter white; ventrolateral areas of body and ventral surface of tail bright lemon-yellow.

The juvenile pattern is present to about 53 mm snout-vent length. Between 53 and 56 mm snout-vent length, the dorsal pattern undergoes an abrupt change. The ground color becomes tan-brown to red-brown (females) or gray-blue to black (males); the black bands and spots become dark brown, brown, tan, and eventually fade into the ground color (Figs. 1 and 2). The yellow of the ventral surface of tail and ventrolateral area of venter fades to dirty white. Adult females become somewhat drab, with white venter and a dull orange-red eye ring (Figs. 3 and 4). Males generally develop small white spots over the entire dorsal surface of the body, and occasionally small spots of blue-green appear on the dorsal surface of the forelimbs and along the sides of the body. The region around the eye becomes vivid orange-red.

The ventral pattern of adult males is slightly different in the northern and southern samples. Adult males from the Punta El Paraiso area have blue-green chins, blue-black throats, ventrolateral areas of chest blue-black, and ventral surfaces of limbs and venter yellow, with a grayish blue suffusion. Adult males from the Paracas Peninsula have deep blue chins, yellowish green throats, with less dark gray suffusion of chest, sides and ventral surfaces of limbs and venter than the El Paraiso sample. The ventral surfaces of the feet in both samples are pinkish tan.

Habitat and natural history. Juveniles of this species were taken from sandy beaches on the Paracas Peninsula, and adults were taken from rocky bluffs from Paracas and Punta El Paraiso. Mertens (1956) indicated that thersiae mainly inhabit sand, but occasionally frequent rocks. Our observations indicate that there is a relatively distinct segregation between juvenile and adult habitats, juveniles prefer sandy substrata while adults prefer rocks. We did not observe this species farther than 500 m from the ocean. A preliminary examination of a few stomachs from the El Paraiso area suggests that thersiae feed very close to water if not in it. All stomachs examined were packed with hundreds of aquatic Hemiptera (waterboatmen).

Ten adult females, ranging from 55 to 62 mm snout-vent length, were taken
from the El Paraiso area on 12 December 1968, and contained one to four (2.8) oviducal eggs or yolked ovarian follicles. Three additional females from 59 to 62 mm snout-vent length taken on the same day, had flaccid oviducts, undeveloped ovarian follicles, and apparently had recently deposited eggs.

Distribution. Tropidurus theresiae is presently known only along the Peruvian coast from about Huacho south to the Paracas Peninsula (Fig. 6). A total of 46 specimens have been examined from the following localities:

Lima. 14 km NW Chancay, RT 48 (in LSUMZ); Cruz de Hueso, USNM 75392; 2 km NW Cerro Azul, LACM 49078-79, TCWC 28608; 13 km S, 7 km W Huacho, LACM 49065-74, TCWC 28594-604, 28920; 3 km NW San Antonio, TCWC 28609; 8 mi SE Chilca, MVZ 85439, 93118; 7 km SSE Chilca, MVZ 85419; 5.5 km NE San Bartolo, MVZ 93119. Ica. 7.2 km S and W Paracas, LACM 49060-63, 49075-77, TCWC 28588-93, 28605-07.

Other locality records (all from Mertens 1956) are: Lima. Pasamayo, near Chancay; between Ancon and Ventanilla; between Puente Piedras and La Ventanilla; Atocongo, near Lima.

TROPIDURUS THORACICUS (TSCHUDI)

St. (etirolepis) thoracica Tschudi 1845. Arch. Naturgesch. 11:156.


Lectotype: ZMB 4318 (Mertens 1956). Type locality: Huacho, Ica, Pisco, and Islay, Peru (here restricted to the vicinity of Huacho, Lima Dept., Peru, see account for T. t. thoracicus below).

Diagnostic characters. Tropidurus thoracicus is a member of the peruvianus group and is distinguished from theresiae by the presence of an enlarged, usually continuous, keeled, vertebral row of scales and the absence of an orange-red eye ring in adult males; from peruvianus and tigris by the presence of two or more rows of scales between the nasal and first labial scales. Furthermore, thoracicus is the only member of the peruvianus group with a distinct black spot in, and extending posterior from, the antehumeral folds. These spots are present in juveniles and adults of both sexes.

The scales on the posterior margin of toes on the limbs are enlarged and keeled, forming a conspicuous fringe. This condition is not present in other members of the genus.

Variation. The variation in size, scutellation, color, and color pattern is such that three morpho-geographical populations are evident. The relative uniformity within and the differences between these apparently allopatric populations are such that the recognition of three races would most adequately reflect their relationships. These races are as follows:

Tropidurus t. thoracicus (Tschudi)

St. (etirolepis) thoracica Tschudi 1845. Arch. Naturgesch. 11:156.

Figure 8. Dorsal view of representative adult male specimens of the three subspecies of *Tropidurus thoracicus*. Bottom to top: holotype of *T. t. icae* new subsp.—LACM 48987, 77 mm S-VL; *T. t. thoracicus*—LACM 48912, 63 mm S-VL; and holotype of *T. t. talarae* new subsp.—TCWC 28507, 70 mm S-VL.

*Lectotype.* Mertens (1956) presented a description of the syntype he designated as lectotype (ZMB 4318) and illustrated the specimen with photographs of dorsal and ventral views. The specimen has a heavily pigmented venter and a low number of relatively large, dark, dorsal spots, and thus, most closely resembles specimens of a series from near Lomas de Lachey (see *Variation*...
below) a locality inland and slightly south of Huacho, one of the cities cited in the "type locality" (Huacho, Ica, Pisco, and Islay). Specimens of *thoracicus* from the vicinity of Pisco and Ica differ from the lectotype and are referrable to a new race described below. No *thoracicus* are known south of the Ica area, and would not be expected to occur as far south as Islay in extreme southern Peru. In general it is appropriate that a type locality be restricted to an area where morphotypes
similar to the type are now found. Applying this to *thoracicus*, our best estimate for the type locality is the vicinity of Huacho.

*Diagnostic characters.* A relatively small, dark race of *Tropidurus thoracicus* differing from other races by the presence of dark pigment (gray to black) on chest and venter, which in adults of both sexes extends onto the underside of the tail and hind limbs (Figs. 8-12). It also differs from the race to the north (*T. i.*
Figure 11. Ventral view of representative adult female specimens of the three subspecies of Tropidurus thoracicus (specimens and order are the same as in Figure 10).

talarae new subspecies) by the presence in both adults and juveniles of a distinct, broad, dark stripe extending from the posterioventral edge of the orbit to at least the level of the axilla and usually to the lateral surface of the tail. Between the axilla and the tail, this line may be interrupted but still marked by large linearly-arranged spots. The race to the south (T. t. icae new subspecies) has a similar lateral stripe, but it is only present posterior to the level of the ear opening and does not extend to the orbit.
Variation. Most of the specimens examined by us are from three areas. The specimens from these areas were grouped into samples for analyses of variation. The Mocupe sample (N = 21) is composed of specimens from the vicinity of Mocupe and Puerto Eten in southern Lambayeque Department. This sample contains the three syntypes of *Tropidurus thomasi* and animals from the northern edge of the range of the subspecies. Southern populations are represented by a sample (N = 12) from the vicinity of Lomas de Lachey, ca 30 km SSE of Huacho, Lima Department. The third sample is composed of specimens from the vicinity of Culebras (N = 67), ca 18 km N of Huarmey, Ancash Department.
Table 1
Data for meristic features of *Tropidurus thoracicus* samples: scales around body (SAB), vertebral crest scales (VCS), fourth toe lamellar scales (TLS), and supraocular scales (SOS). Data are mean ± standard error, range in parentheses and number of specimens in sample.

<table>
<thead>
<tr>
<th></th>
<th>SAB</th>
<th>VCS</th>
<th>TLS</th>
<th>SOS</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>talarae</em></td>
<td>131.6 ± 1.86</td>
<td>83.7 ± 1.42</td>
<td>23.9 ± 0.33</td>
<td>10.6 ± 0.34</td>
</tr>
<tr>
<td></td>
<td>(118-147)</td>
<td>(75-97)</td>
<td>(22-27)</td>
<td>(8-13)</td>
</tr>
<tr>
<td></td>
<td>N = 50</td>
<td>N = 50</td>
<td>N = 51</td>
<td>N = 50</td>
</tr>
<tr>
<td><em>thoracicus</em></td>
<td>133.3 ± 2.24</td>
<td>65.1 ± 1.90</td>
<td>25.6 ± 0.65</td>
<td>9.8 ± 0.47</td>
</tr>
<tr>
<td>Mocupe</td>
<td>(125-140)</td>
<td>(60-76)</td>
<td>(23-29)</td>
<td>(8-11)</td>
</tr>
<tr>
<td></td>
<td>N = 19</td>
<td>N = 21</td>
<td>N = 21</td>
<td>N = 21</td>
</tr>
<tr>
<td>Culebras</td>
<td>128.1 ± 1.76</td>
<td>72.2 ± 1.40</td>
<td>26.5 ± 0.45</td>
<td>8.2 ± 0.25</td>
</tr>
<tr>
<td></td>
<td>(111-148)</td>
<td>(62-89)</td>
<td>(21-30)</td>
<td>(6-11)</td>
</tr>
<tr>
<td></td>
<td>N = 67</td>
<td>N = 67</td>
<td>N = 67</td>
<td>N = 67</td>
</tr>
<tr>
<td>Lomas</td>
<td>130.5 ± 3.94</td>
<td>66.7 ± 2.29</td>
<td>24.3 ± 0.68</td>
<td>9.6 ± 0.99</td>
</tr>
<tr>
<td></td>
<td>(120-138)</td>
<td>(60-72)</td>
<td>(23-26)</td>
<td>(8-12)</td>
</tr>
<tr>
<td></td>
<td>N = 12</td>
<td>N = 12</td>
<td>N = 12</td>
<td>N = 12</td>
</tr>
<tr>
<td><em>icae</em></td>
<td>136.0 ± 2.88</td>
<td>74.1 ± 1.63</td>
<td>31.1 ± 0.55</td>
<td>11.0 ± 0.39</td>
</tr>
<tr>
<td></td>
<td>(116-165)</td>
<td>(61-87)</td>
<td>(26-39)</td>
<td>(7-14)</td>
</tr>
<tr>
<td></td>
<td>N = 63</td>
<td>N = 61</td>
<td>N = 63</td>
<td>N = 63</td>
</tr>
</tbody>
</table>

Scutellation. Significant differences obtain between the three samples of *T. t. thoracicus* (Table 1). Despite these differences, the three samples tend to be relatively more similar to each other when compared to samples of the other subspecies. The means for most features are either intermediate or smaller in value than those of the other subspecies. The greatest difference between the means of the three samples in vertebral crest scales from occiput to rump (VCS) is 7.1; whereas, the difference between the closest mean for a sample of *thoracicus* to that of *talarae* is 11.5. No geographic trends in scutellation are detectable within the three samples or within the species. The Culebras sample has the lowest mean values for SAB and total number of supraocular scales (SOS) of all samples and the highest values for VCS and fourth toe lamellar scales (TLS) of the three samples of *thoracicus*. The latter two values, however, are significantly lower than those of the samples of the other subspecies. When means for features are compared between the geographically closest samples of other subspecies, some of the greatest differences are apparent. For example VCS for *talarae* and Mocupe (83.7 and 65.1) and TLS for Lomas and *icae* (24.3 and 31.1).

Color and Color Pattern. Specimens of both sexes have a dorsal ground color of dark gray to dark brown with relatively large black or brown spots and flecks of white. The area of and adjacent to the vertebral row of scales is darkened, tending to form a mid-dorsal stripe. Animals from the southern part of the range have more grayish brown ground color and relatively fewer and larger
spots. Animals from the area of Culebras are darkest dorsally. The dorsal coloration extends onto tail, with the spotting on the lateral surfaces of tail tending to form undulating or zigzag patterns and stripes. Ventrally, all specimens have a heavy suffusion of dark gray to black color in the gular and upper chest area, more intense in adults. Adults of both sexes have a suffusion of gray to black color extending from the chest region posteriorly onto venter. This color is noticeably lighter than that of the gular region and is frequently divided to form lateral streaks. The intensity and extent of color is greater in males, where it frequently extends posteriorly onto the tail and hind legs. The chin and infraorbital areas are mottled, most apparently so in juveniles and females, with brownish gray on a light background. Laterally there is a prominent broad, dark stripe that begins ventral to the orbit and extends posteriorly along the body to the hind legs and frequently onto the tail. Occasionally there is an indication of a thin dark stripe extending from the posterior edge of eye to above the forelimb insertion; usually, however, this "stripe" is represented by a row of dark spots. Occasionally, as in the sample from Lomas de Lache, the body stripe is vague or nearly absent, being replaced by spotting, but the stripe is prominent between the orbit and forelimb in all specimens.

_Tropidurus t. icae_ new subspecies

_Holotype._ LACM 48987 from 12 km NE (rd), Ica, Ica Dept, Peru. Collected 15 December 1968 by James R. Dixon and John W. Wright (field members P2064 and PK 147).

_Paratypes._ See Distribution below.

_Diagnosis._ A relatively large race of _thoracicus_, which differs from other races by having dark (brownish to gray) streaks of color, usually forming radiating lines or chevrons, on the gular and throat region and extending onto the labials. The pectoral and gular region in adults, especially males, frequently darkened (slate gray) but never to the extent of masking the streaking. In addition, it differs from _T. t. thoracicus_ in lacking the dark pigment on the venter and the ventral surface of the tail, ventral surface of tail is light blue in adults rather than gray to black; and differs from _T. t. talarae_ new subspecies in that a dark lateral stripe is apparent on body, but is more a series of slightly overlapping dark spots than a continuous stripe. No striping is apparent anterior to the ear opening as in _T. t. thoracicus_.

_Description of Holotype._ Adult male (Figs. 8, 9, and 12) S-VL, 77 mm.; SAB, 125; scales in vertebral row from occiput to rump, 72; fourth toe lamellae, 29; and five supraocular scales over each eye. Ground color grayish brown with small brownish spots on dorsum, tending to form transverse rows, spots continuing onto lateral surfaces of body. Areas between spots with small irregular flecks of white. Dorsal pattern extending onto tail with spots tending to fuse into rings on distal portion. Dorsal surface of forelimbs irregularly barred. Dorsal surfaces of hind limbs with the color and color pattern of dorsum. A broad dark lateral stripe extends from above the point of insertion of the forelimb to the base of the tail. Color is intensified where spots occur along stripe. Dorsal surface of head brown-
ish gray with an indication of an interorbital bar. Parietal eye ringed with white. Side of head with the dark ground color with streaks of both lighter and darker colors, an indication of a dark stripe through eye. Chin, gular and pectoral regions mottled or streaked with gray on a light background, with an indication of radiating stripes in gular region. Antehumeral fold with black spot. Chest and venter immaculate. Ventral surface of tail light blue.

Variation. All known specimens of this race are from a relatively small area in the vicinity of Ica, Ica Dept. All specimens were grouped into a single sample for analyses of variation.

Scutellation. Data for meristic characters analyzed are presented in Table 1. Means for three out of four characters (SAB, TLS and SOS) are significantly higher (Student's t) than those of other races. For the remaining character, VCS, only the mean from the sample of talarae is higher than that of icae. The range of TLS (26-39) is higher than the means of all samples except that of the Culebras sample of thoracicus.

Color and Color Pattern. The dorsal ground color in both sexes is grey to brown with small dark brown spots arranged in nearly transverse series. Smaller more numerous white spots present between dark ones, tending also to form transverse rows. Mid-dorsal row of scales either conspicuously darker or lighter than the adjacent ground color. Laterally there is usually a wash of brown color extending from the posterior edge of ear opening to the level of the hind leg insertion, sometimes continuing as an ill-defined stripe onto base of tail. Dorsal spots within this wash are larger and darker and impart a range of effects from a linear series of large spots to loosely connected dark spots to a zig-zag stripe to a continuous stripe highlighted with darker spots. The dorsal color pattern extends onto the corresponding surface of the hind legs and tail. Ventrally, all specimens have conspicuous black pigment in the antehumeral fold. The venter and ventral surface of hind limbs immaculate. The distal two-thirds of the tail is light blue, more intense in adult males. The gular and chest areas of hatchlings and juveniles are sparsely marked with grey-brown color, tending to form mottled chevrons on the throat and chin. Adults of both sexes have more grey to brown pigment on the chest and gular area but not to the extent of masking the chevron pattern. The black in the antehumeral fold is never masked even in the most heavily pigmented individuals. Sides of heads and labial areas mottled, with a general tendency for dorsal-ventral streaking of brown color that is often connected with that of the gular area.

_Tropidurus thoracicus talarae_ new subspecies

_Holotype._ TCWC 28507, from 2 km N Talara, Piura Dept, Peru. Collected 3 December 1968 by John W. Wright and James R. Dixon (field number P 1313).

_Paratypes._ See Distribution below.

_Diagnosis._ A relatively large race of _thoracicus_ differing from all other races by the lack of a dark lateral stripe on body; side of head and neck with two thin dark stripes, one beginning posterior to the eye and one ventral to eye, separated by a conspicuously lighter, unmarked area; striping usually terminates at the level
of the insertion of the forelimb. In addition, it differs from *T. t. thoracicus* in lacking the dark pigment on the venter and ventral surfaces of tail and hind limbs; and it differs from *T. t. icae* in lacking the blue color on the tail, the color of the ventral surface of tail is undifferentiated from that of venter; and in lacking large lateral spots.

**Description of Holotype.** Adult male (Figs. 8, 9, and 12) S-VL 70 mm.; SAB, 146; scales in vertebral row from occiput to rump, 71; fourth toe lamellae, 24; six supraocular on left and seven on right side of head. Ground color of dorsum gray with small black spots tending to form transverse rows, and smaller dark spots tending to form longitudinal series. Area between spots with numerous irregular flecks of white. Dorsal pattern extends onto upper surfaces of tail and hind limbs. Dorsal surface of forelimbs irregularly barred. Lateral surface of body colored like dorsum. Side of head and neck with a pair of fine dark stripes, one beginning posterior to eye and one ventral to eye. Both stripes terminate posteriorly at the level of the insertion of forelimbs. Area between stripes unspotted and lighter than ground color. Dorsal surface of head brown with an indication of pre- and postorbital bars. Chin and infralabial areas immaculate. Gulars, upper chest and ventral surface of forelimbs with considerable black color. Ventral surfaces of body and tail immaculate.

**Variation.** Specimens of this race are known only from two adjacent localities in the immediate vicinity of Talara, Piura Dept. Specimens from these localities were grouped into a single sample for analyses of variation.

**Scutellation.** A majority of the specimens in the sample have incomplete vertebral series of scales. Counts of these scales were made in two ways, first only the enlarged scales were counted, and second, all scales in the vertebral row were counted whether or not they were larger than adjacent dorsal scales. These two counts yielded significant differences (71.5 ± 1.54 and 83.7 ± 1.42). In this sample scales are relatively smaller than those of other samples and most specimens in other samples have complete series, we have used the total count to best reflect these differences. As such, this sample has the highest number of VSC of any sample. Otherwise this sample does not differ greatly in other features of scutellation from the other samples except in TLS, where it has the lowest mean.

**Color and Color Pattern.** Hatchling and juvenile individuals of this race have nearly immaculate ventral surfaces, with only a small amount of dark flecking in the gular and upper chest areas in some individuals. With age, the central gular area becomes darker extending back in the form of a triangle to just beyond the antehumeral area and onto the upper chest. In females, pigment development usually stops at this point, whereas males develop considerable dark pigment in both area and intensity. In adult males (Fig. 9), the black of the antehumeral fold blends completely with that of the chest and gular region. The edge of the lower jaw remains clear of dark pigment as does the venter and ventral surfaces of the hind legs and tail. The dorsal color pattern consists of two series of small dark (grey to black) spots, the larger series tends to form a transverse series and the smaller is arranged in a more longitudinal manner; and scattered white spots forming no apparent pattern. The vertebral row is not colored differently from
the adjacent dorsum, but both the white and dark spots are more intense when they occur on the midline, tending to form alternating light and dark dashes throughout the length of the vertebral series.

**Comparisons.** Comparative statements for features of scutellation are presented above in the Variation section of each subspecies. We present below a key that emphasizes the salient features of the color and color patterns of each subspecies.

**Key to the Subspecies of Tropidurus thoracicus**

1a. A broad dark, lateral line or linearly arranged dark spots present on body and extending forward to level of eye or ear opening ................. 2

1b. No dark, lateral line or spots on body ..............................  T. t. talarae

2a. Chin and labial scales unpatterned; dark lateral line on body reaching orbit, venter darkly pigmented in adults ......................  T. t. thoracicus

2b. Chin and labials striated, mottled or with dark flecks of pigment; dark lateral line on body not reaching edge of orbit; venter immaculate ........  T. t. icae

**Body Size.** Body size was compared utilizing the S-VL for the five largest females and five largest males in each sample population. In no sample is the largest female as large as any of the largest males. Overall the females average 9 to 18 mm less than males. The largest lizards occur in icae with a mean size of 85.6 (77-94) for males and 74.2 (70-76) for females. Body sizes in samples of thoracicus are much smaller with 65.2 (66-67) and 56.8 (54-59) for Lomas, 65.8 (63-68) and 55.4 (52-62) for Culebras and 70.6 (66-74) and 51.8 (48-56) for Mocupe. Sizes in talarae are larger than in thoracicus with 81.6 (77-84) for males and 63.4 (60-70) for females. Sexual dimorphism is greatest in talarae. Thus the northern and southernmost animals are largest, with markedly smaller animals in the intervening area. The smaller animals are also the darkest and are from areas with greater “fog shrouding.” Both the smaller size and darker color may be adaptations for shorter thermally optimal activity periods.

**Habitat and natural history.** Lizards of this species were found only in sandy areas with considerable vegetation. An examination of stomach contents of specimens of each race collected in November and December indicated that, at least as adults, they are mainly or exclusively vegetarians, feeding largely on the flowers, immature fruits and leaves of mesquite and acacia. None was observed to climb, but several were observed to “sand swim”. That is, they would dive head first into sand and rapidly wedge or “shimmy” themselves into the sand, as do species of the North American genus Uma. Lizards of this genus also have a fringe of scales on the posterior margin of hind toes.

Females apparently mature at about 45 to 50 mm S-VL and lay from one to five eggs per clutch. The average number of yolked ovarian follicles or oviducal eggs in 40 females was 3.1. Yolked follicles were present in females taken in mid-November and shelled oviducal eggs were present in specimens collected in early to mid-December.
Distribution. The range of thoracicus apparently is disrupted forming three isolated populations corresponding to the races described above (Fig. 6). No specimens are known from the Sechura Desert from Mocupe to Talara, despite considerable collecting in this relatively continuous, apparently suitable habitat. Little suitable habitat is present from the area north of Ica to Lima on the north. Several isolated patches of vegetation were investigated in this area but no thoracicus were observed. This species is not known from north of the immediate vicinity of Talara nor south of Ica.

Specimens have been examined from the following localities:

\textit{Tropidurus t. thoracicus}.—\textbf{Ancash}. 2 km N Culebras, LACM 48952-74, TCWC 28519-41; 18 km N Huarmey, LACM 48910-19, RT (in LSUMZ) 80-93, TCWC 28475-85; 23.8 km SSE Huarmey, LACM 48975-79, RT (in LSUMZ) 68-70, 358, TCWC 28542-47. \textbf{Lambayeque}. Eten, BMNH 1946.8.29.58-60; 3 mi NW Mocupe, MVZ 11106-73; 7 km SSE Mocupe, MVZ 82376, 82401-02; 26.5 km N Chepen, LACM 48920-24, TCWC 28487-92. \textbf{Libertad}. 2 km S Chicama, TCWC 28486; 2.3 km S Jequetepeque, LACM 48951, TCWC 28493; Trujillo, (Mertens 1956). \textbf{Lima}. 23 km N, 4 km E Chancay, LACM 48980-85, TCWC 28548-53. Literature locality records (Mertens 1956). \textbf{Ancash}. Near Puerto Casma, km marker 333 south of Casma. \textbf{Lima}. Ventanilla; Atocongo; Villa; Lurin; Pucusana.

\textit{Tropidurus t. icae}.—(all paratypes) \textbf{Ica}. 12 km NE Ica, LACM 48995-05, TCWC 28564-74; 16 km NNW Pozo Santo, LACM 48986-94, 49014-15, TCWC 28554-63, 28585-86; 6.3 km ESE Pozo Santo, LACM 49006-13, TCWC 28576-84; 1 km SSE San Jose de los Molinos, TCWC 28575.

\textit{Tropidurus t. talarae}.—(all paratypes) \textbf{Piura}. 2 km N Talara, LACM 48925-45, TCWC 28474, 28494-514; 3 km S Talara, LACM 48946-50, TCWC 28515-18, 28587.

\textbf{TROPIDURUS TIGRIS} (TSCHUDI)

\textit{Steirolepis tigris} Tschudi 1845. Arch. Naturgesch., 11:156


Holotype: Lost, see Mertens (1956). Type locality: Huacho, Ica, Pisco, and Islay, Peru (restricted to the coastal foothills and mountains of Peru, between Huacho and Islay by Mertens 1956).

Diagnostic characters. \textit{Tropidurus tigris} is a member of the \textit{peruvianus} group, differing from \textit{thoracicus} by the presence of one row of scales between the nasal and the first labial scales (rather than two or more rows); from \textit{theresiae} by the presence of a slightly enlarged vertebral row of scales; from \textit{peruvianus} by the presence of transverse rows of black spots on the throat of males rather than dark chevrons, and by the presence of large keeled scales with a free posterior spine on the dorsal surface of the brachium.

Variation. An examination of 68 specimens from throughout the known distribution of the species indicates slight variation in color pattern and in some scale characters. The number of scales around the body range from 121 to 157 (140.4); number of fourth toe lamellae, 25 to 33 (28.6); number of scales of the vertebral row, 72 to 98 (86.3); snout-vent length of adult males range from 55 to 105 mm (70.6), females from 50 to 72 (61.5).

The ventral color of adult male \textit{tigris} is generally a mixture of orange-red, bright yellow, black, white, and pale bluish green. The ground color of the throat
and chin is orange-red with some bright yellow near the shoulder; each black spot of the throat is surrounded by one row of white granules; the antehumeral fold is black, the black reaching almost to the center of the upper chest in adults. The ground color in the region from the throat to the center of the chest is white, with or without scattered areas of black intermixed. Small patches of scales in the ventrolateral body areas are pale orange, yellow, bluish green, sooty black and burnt orange hues. Ventral surfaces of hind limbs and pelvic region are white in juveniles, gradually becoming washed with sooty black in large adults. The ventral surfaces of tail are pale bluish green (Figs. 1 and 2).

Adult female tigris are drab, with less distinct dorsal markings and the venter is usually gray, white or cream (Figs. 3 and 4). The throat spots are usually fused into a series of loosely connected, transverse lines. The spots are never as distinct as in males, and often have ill-defined margins.

**Habitat and natural history.** T. tigris is an inhabitant of foothills where rocks and boulders are abundant, but vegetation sparse. The elevational range of the species is from sea level to approximately 2,800 meters.

Adult females of tigris were found to contain two to five (3.8) yolked ovarian follicles or oviducal eggs during the months of September, November, and December. The smallest female with yolked ovarian follicles was 49 mm in snout-vent length, the largest 72 mm.

**Comments.** Mertens (1956) recognized the distinctive morphology of tigris but interpreted the occasional partial fusion of spots on the throat of males to be evidence of intergradation with peruvianus. After analyzing larger samples of both populations, we see no evidence of gene exchange. Although we did not observe the two species in sympatry, the evidence indicates that they do occur together. The ranges of the two are parallel for over 1,000 km and specimens of each were taken by us at localities separated by only 3 km in the vicinity of San Antonio south of Lima. Locality data for other specimens indicate that the two are broadly sympatric adjacent to the scattered coastal hills in the vicinity of Callao and Lima.

**Distribution.** Tropidurus tigris is found throughout the Peruvian coastal foothills and Andean slopes from the vicinity of Trujillo south to at least Chala, an airline distance of some 1,000 km, and between the elevations of near sea level to 2,800 m (Fig. 6). The geographic range is not known south of Chala. It is possible that tigris may be found as far south as northern Chile (Donoso-Barros 1966).

We have examined 86 specimens from the following localities:

No specific locality USNM 5715 (2). Ancash. 39.7 km NNW Pativilca TCWC 28647-49; Huaras, 3,200 m, BMNH 1900.6.20.5-6; Shigiyay, 1,600 m, BMNH 1900.6.20.4. Lima. 2 km ESE Asia LACM 48830-34, TCWC 28662-66; 9 km SSE Cañete LACM 48837-38, TCWC 28669-71; 6.6 km WSW Circon LACM 48839, TCWC 28672-73; Chosica USNM 75415-24; Lima USNM 75400; Lomas de Lachey MVZ 82334, 82337, 82391-92; 2 km N, 3 km E Naña MVZ 82389; 20.3 km NNW Quilmana LACM 48835, TCWC 28667; 12.1 km N Quilmana LACM 48836, TCWC 28668; Río Rimac Valley USNM 51517-18; 2.3 km NE Santa Eulalia LACM 48840-50, TCWC 28674-84; Surco USNM 75393; Verrugas Canyon USNM 51519-20, 75394-97. "sandy hills around Lima," BMNH 63.2.3.20; Lima, BMNH 75.2.13.1; Callao, BMNH 1900. 11.27.27 Huancavelica. 2 km E Ticrapo MVZ 83689. Ica. 40 km S Nazca, MVZ 57809; 1 km ESE San Jose de los Molinos, TCWC 28652. Arequipa. 10 km S Chala, MVZ 57805-07.
Other localities (Mertens 1956) are Libertad, Membrillar, Ancash, Yautan, Lima, Lachay, San Bartolome, Zarete, Atocongo, Valle de Cañete, Arequipa, near Chala, between Sachabamba and Ocaña.

**TROPIDURUS OCCIPITALIS GROUP**

**TROPIDURUS KOEPCKEORUM** Mertens


**Holotype:** SMF 50337, adult male. Type locality: above Pariacoto, 1600 m, Department of Ancash, Peru.

**Diagnostic Characters.** *Tropidurus koepckeorum* is a member of the *occipitalis* group and as such differs from members of the *peruvianus* group by having imbricate, keeled and mucronate dorsolateral body scales. It differs from *occpitalis* by lacking distinct occipital spots, by having distinct spots in the gular region and differing in scutellation by having more than 65 scales around mid-body, rather than 60 or less, and the postmental shields are larger than the first pair of chin shields. It differs from *stolzmanni* in having large dumbbell-shaped spots laterally displaced along the middorsal crest and having distinct spots in the gular region, rather than lines forming chevrons, more distinct in males.

**Variation.** Essentially no differences in scales counts could be found between samples from Motupe and 18 km N Olmos. The number of scales around the body range from 66 to 80 (73.5) and 71 to 77 (74.4), respectively.

The number of enlarged vertebral (crest) scales ranges from 45 to 55 (48.7) on lizards found east of Olmos and 47 to 52 (48.9) on those just south of Motupe. Only two specimens were examined from near the type locality and the scale counts of both are well within the range of variation at the former locality.

Adult male color pattern from south of Motupe consists of a series of two to four, thin, transverse black lines across the nape and shoulders, followed by a series of small, dorsolateral black spots, connected to the opposite spot or the following spot on the opposite side of body, by a series of loosely connected smaller black spots (Fig. 13). Occasionally, the first three transverse lines behind the occipital scale form a linear series of black dots rather than continuous lines. The ground color of the head, dorsum, and hind limbs is usually yellowish tan, but occasionally tan to brown. The hind limbs usually lack black spots; forelimbs with black bands or spots; antihumeral fold black; side of head with a series of four crescent-shaped black marks, the first beginning just behind nostril, the last below eye to edge of throat; a series of black spots between eye and ear, and along outer edge of supraoculars; vertebral crest white; venter white from midbody to below tail; suffusion of tan-orange ventrolaterally, from arm to posterior third of body; usually a yellowish orange wash across venter behind arms; area between throat and arms usually white with a suffusion of black spots; posterior part of throat black, surrounded laterally and anteriorly by series of black dots on white ground color of chin and pinkish tan ground color around black throat spots (Fig. 14).
Females with ground color tan or brown with an ill-defined series of dark gray, paravertebral spots; paravertebral dark spots larger than those in males, but not as sharply defined; limbs unspotted; head usually mottled with dark gray and tan; vertebral crest low with series of 15 to 20 small black dots on ground color; no sharply defined, black crescent marks on side of head; eye with reddish orange ring; rostral and labials with reddish orange tint; reddish orange area from labials to ear and partly on side of neck; antehumeral fold black; anterodorsal part of forearm with diffuse black areas; throat with diffuse black spots on lemon yellow to greenish yellow ground color (Figs. 15 and 16).

Adult males from near the type locality are generally darker in ground color with brighter colors on the venter and head than those from the Motupe and Olmos areas. However, the basic pattern of dorsal spots, throat dots and spots, and forearm markings are the same in all samples.

Habitat and natural history. Mertens (1956) mentioned that he found specimens in mesquite groves, in a stone and gravel semi-desert, and on rocks or in the scrub in a cactus semi-desert. All of the specimens taken by us were from granite boulders or on the ground near granite boulders. The vegetation of the Motupe area consists of Cereus, Capparis (tree form), Prosopis, Cercidium, and Opuntia, with little ground cover of any kind. The vegetation of the area east of Olmos consists of a large number of trees and shrubs with a denser ground cover, especially along the dry stream course.

Several individuals were found at night beneath exfoliating flakes of large granite boulders, as high as 2 m above the ground. Most individuals sought cracks or flakes on boulders for hiding places during the day.

An examination of the ovaries and oviducts of females indicated that they reach sexual maturity at about 50 mm snout-vent length. Reproductive conditions of females taken during August 1967, and November and December 1968, indicated that there is at least a winter and spring reproductive period. The number of yolked ovarian follicles and oviducal eggs ranged from 2 to 4 (3.0) in females with snout-vent lengths from 50 to 68 mm. Males apparently mature at a much larger size, based upon breeding colors and other secondary sex characters. The smallest mature male examined was 64 mm snout-vent length, whereas the largest male measured 81 mm.

Comment. Burt and Burt (1931) were the first to note that individuals referable to occipitalis and koepckeorum were sympatric at Chongolappi, Peru. They interpreted the individuals of koepckeorum as representing intergrades between occipitalis and bocourtii (= stolzmanni).

Distribution. The known elevational range of koepckeorum is from 285 m at Sierra de la Vieja (near Motupe), to 2100 m at Membrillar (near Casma). The geographic distribution of the species is from the foothills along the eastern side of the Sechura Desert, south to the Rio Shigiyaj area (Fig. 6). A total of 86 specimens have been examined from the following localities:

Piura, Chongolappi, AMNH 28603-05, 28607-08. Cajamarca. 16 km NE Chongoyape, RT 95-96 (in LSUMZ); 25 km NE Chongoyape, RT 100 (in LSUMZ). Lambayeque. 7 km S Motupe (Sierra de la Vieja), LACM 49080-87, TCWC 28686-89; 21 km N, 18 km E Motupe
LACM 49088-104, TCWC 28440-44, 28707, 28690-706; 4 mi SSW Motupe, MVZ 119242, 119252-54; 21 km E, 7 km N Olmos, MVZ 82397-99, 119241, 119250-51; 12 mi ENE Olmos, MVZ 119238-40, 119246-49; 17 km E, 6 km N Olmos, MVZ 82335; 19 km E, 6 km N Olmos, MVZ 82394-96; 82360; 3 mi N Oyotun, MVZ 119243-44; 8 mi E of Eten, BMNH 1900.6.20.7. Libertad. Poroto, LACM 109569. Ancash. 66 km E Casma, MVZ 82345, 82390; Rio Shigiy, 1600 m, BMNH 1900.6.20.7.

Other Peruvian records (Mertens 1956) are: Libertad. Pariakoko. Lambayeque. Olmos, Membrillar, El Tambo.

**TROPIDURUS OCCIPITALIS** Peters


*Holotype*: BMNH 6646, male. Type locality: Peru

*Diagnostic Characters.* *Tropidurus occipitalis* is a small member of the *occipitalis* group and differs from the other members, *koepckeorum* and *stolzmanni*,...
by having a distinct dark occipital spot and by lacking both spots and lines in the gular region; differing also from *stolzmanii* in having distinct dorsal spotting and by having fewer than 70 scales around midbody, rather than 80 or more.

**Variation.** Adult males range from 50 to 75 mm (64.4) and adult females from 47 to 58 mm (52.2) in snout-vent length. Males have a series of three to six large black blotches on the anterior part of dorsum, while females have a series of seven to 10 small spots from the nape to level of hind limbs, or a uniform pattern.

The color and pattern of male *T. occipitalis* consists of the throat and chin without dark spots, usually with a diffuse wash of gray and pink on throat, varying to reddish pink in some specimens; venter either grayish tan, gray, or reddish orange, with a series of reddish brown and blue-green flecks along the ventrolateral surfaces; some males have a light orange-yellow suffusion on chest and venter; antehumeral fold black; dorsal ground color bright golden tan,
golden brown, reddish brown or combinations of these colors; dorsolateral areas
dull brown, grayish brown or slate; black rhomboid or diamond-shaped blotches
from nape to posterior third of body, sometimes restricted to anterior third of
body; region around eye occasionally reddish orange and an occasional reddish
orange spot on nape; small black occipital spot always present (Figs. 13 and 14).

The ground color of the dorsum of adult females ranges from light tan to
gray brown; dorsum sometimes unicolored, but usually a series of small dark
brown, vertebral spots are present (Fig. 15). Juvenile females have diffuse lateral
and dorsal dark markings; chin and throat of adult females dirty white to gray
with a pinkish red throat spot (Fig. 16); venter dirty white to yellowish white in
juveniles and adults.

Habitat and natural history. The majority of specimens were found on or near
small boulders, trees, and shrubs. Several were found under debris associated
with abandoned human dwellings. Most were found in habitats with some kind of
vegetation, such as mesquite, acacia, Capparis scabrida, dense beach shrubs or semiarid woodlands of the foothill slopes.

This species is primarily scansorial; most specimens were taken one to three dm above the ground on trees. However, some were taken on the ground in the vicinity of shrubs where they appeared to be foraging for food.

Females collected in late July, early August and mid-November contained shelled, oviducal eggs. The number of yolked ovarian follicles and oviducal eggs ranges from 2 to 4 (3.5), with unyolked ovarian follicles ranging from 19 to 29 (24.5). Females apparently mature between 45 and 47 mm, and males between 50 and 55 mm snout-vent length.

Distribution. Tropidurus occipitalisranges in elevation from sea level to 700 m, and from the arid woodlands of western Ecuador south to the Rio Casma area (9° 30' S) of western Peru (Fig. 6). A total of 177 specimens have been examined from the following Peruvian localities.
**Tropidurus stolzmanni** Steindacher


**Syntypes**: NMW 18908:1, 2. Type locality: Chota, Peru.

**Diagnostic Characters.** *Tropidurus stolzmanni* is a member of the *occipitalis* group and differs from the other members of the group by lacking middorsal spots and by having chevron-shaped lines in the gular region, more prominent in males; differing also from *occipitalis* in lacking an occipital spot. Adult males of *stolzmanni* differ from males of both *koepckeorum* and *occipitalis* in having a broad, black-bordered, white stripe from the eye to near midbody.

**Variation.** Based on body size, there are two populations of this species in the inter-Andean basins of northwestern Peru. One population occurs at intermediate elevations of 1100-1400 m in the upper valleys of the Rio Marañon and Rio Huancabamba. The males of this population have a snout-vent range of 50 to 123 mm (107.1), females 49 to 81 (63.5); with 88 to 102 (92.1) scales around midbody. The second population is found at elevations of 475 to 600 m, in the lower valleys of the Rio Marañon, Rio Huancabamba, Rio Utcubamba and Rio Chinchipe. The males of this population have snout-vent lengths of 52 to 106 mm (80.3), females 48 to 68 (57.4); with 81 to 90 (85.8) SAB.

The color patterns of the males of the two populations are similar. Males have diffuse black, slightly “V” shaped bars beneath the chin (Fig. 14). The bars appear to be loosely connected and alternating with light orange interspaces. The
throat is black, the black extending onto the upper part of the chest. The remainder of the chest and all of the abdomen is pale orange-pink. Some specimens have the black bars of the throat diffuse, with gray interspaces rather than orange and the upper chest grayish white. The lower chest and venter are shades of grayish pink or grayish orange. The ventrolateral areas of the body are diffuse gray or slate. The nuchal crest spines are white. There is a wide grayish white line, bordered on either side by black lines, from the posterior corner of eye to beyond shoulder, fading posteriorly. The ground color of the dorsal and lateral surfaces of head and body are bluish gray with numerous intermixed white spots (Fig. 13). Males have an orange spot from below eye to the edge of the lips, bordered anteriorly and posteriorly by black lines. The labials are usually mottled with black and white, or the black bands of the throat extend through the labials. The eye has a diagonal black line passing through its center.

The color patterns of the females of the two populations are similar. The chin of the female is cream yellow with the throat orange-red (Fig. 16). The venter is grayish white or white. The cream-yellow of the chin extends dorsally and covers side of head from the nostril, and below eye, to over the ear, but seldom extends posteriorly beyond the antehumeral fold. The antehumeral fold is black. The eye is encircled by an orange-red ring. The dorsal and lateral surfaces of body have diffuse slate brown bands on a light grayish brown ground color (Fig. 15). White spots are scattered over the sides, less so in the middorsal area. Dorsal surface of head is frequently blackish brown and generally darker than rest of body.

**Habitat and natural history.** *Tropidurus stolzmanni* is primarily scansional, occurring on rock piles, branches of shrubs and cacti, piles of brush cleared from fields and on fallen trees. These lizards were most active during midmorning hours.

Females from 65 to 76 mm in snout-vent length contained 3 to 4 oviudacal eggs. All oviducal eggs examined were shelled and apparently ready for deposition. One female 73 mm in snout-vent length contained 16 unyolked ovarian eggs. These lizards were taken between 23-28 November 1969.

**Distribution.** This species is apparently restricted to the semiarid foothills and valleys of the inter-Andean basins of northwestern Peru (Fig. 6). The following specimens (129) have been examined from Peru:

- **Amazonas:** 3.5 km SE Bagua Grande, LACM 49129-30; 8 km WSW Bagua Grande, MVZ 82406; 24 km S Bagua Grande, LSUUM (field nos 350-53); 3.5 km E junction of Bagua Chica and Bagua Grande road, TCWC 28463-64. **Cajamarca:** Bellavista, AMNH 28497-500; USNM 75962-64; 0.5 km S Bellavista, LACM 49116-28, TCWC 28455-61; 1 km N Bellavista, LSUUM (field no 201). 4.8 km S Bellavista, TCWC 28462; El Arenal, MVZ 82408; El Tambo, MVZ 82387, 82400; 4.5 km W El Tambo, LACM 49105; 13 km SSE Hacienda Molino Viejo, LACM 49106-08, 49131-38, TCWC 28445-46, 28465-79; 5 km SE Jaen, LSUUM (field nos 108-12); 9 km S Jaen, LSUUM (field nos 117-29, 140-45); 11 km WNW Las Juntas, LACM 49109-15, TCWC 28447-54; Perico, AMNH 28452-53, 28626-32; 5 km SSE Pomahuaca, MVZ 82336, 82403-05; 28 km N Santa Cruz, LSUUM (field nos 178-79, 202). **Piura:** 16 km W San Felipe, MVZ 82407.

Other known localities: **Cajamarca:** Querocotilla (Burt and Burt 1931); San Pablo (Mertens 1956). **Chota:** “Chota” (Steindachner 1891).
ECOLOGICAL RELATIONSHIPS AMONG SPECIES OF TROPIDURUS IN PERU

Along the Pacific Coast of South America are some of the world's driest habitats. In Peru, rain shadows are produced along the coast not only by the Andes to the east, but by the presence of the offshore, cold-water Humboldt Current as well. As a result, measurable precipitation is essentially absent over much of the coastal zone. Some areas are without rain for years if not decades (Holdridge 1964; Dawson 1963). In general the coastal area from the Sechura Desert south into Chile lies in these shadows. Three plant formations are recognized in this area (Weberbauer 1936). The largest is a broad area with no or only isolated plants termed Desert. This area is interrupted by the two remaining plant formations: the Lomas, consisting of isolated, elevated coastal areas that are frequently fog shrouded and receive moisture from condensation and drip, supporting ephemeral herbs; the Riparian communities of trees, shrubs and herbs adjacent to streams originating high in the Andes. The Sechura Desert receives small, irregular amounts of rainfall. The vegetation of this area, characterized by evergreen shrubs and few if any herbs, is not dependent on direct rainfall, but depends largely on the relatively high water table fed by streams terminating along the eastern and northern margins of the desert. To the north of the Sechura Desert the Humboldt Current swings away from the coast, resulting in a decrease in the shadow effect, and the area receives greater and more regular rain. This area is characterized by thorn scrub vegetation with marked wet and dry seasons. This vegetation zone also extends southward along the foothills north and east of the Sechura Desert. The foothills south of the Sechura Desert are either totally barren or vegetated by widely spaced cacti, a few deciduous shrubs and ephemeral herbs depending on the extent of fog shrouding and/or the occurrence of infrequent rains. The desert on the western slope of the Andes extends from the coast to ca 2,000 m, where it is replaced by the xerophyllus zone of cacti and Franseria and this by tola shrub communities (Weberbauer 1936).

The distributions of all of the species of Tropidurus in Peru, except stolzmanii, are within the coastal desert and foothills, extending from sea level to about 3,000 m. Tropidurus stolzmanii occurs in the xeric interandian valleys of the Rios Marañan, Chinchipe, Utcubamba, and Huancabamba, which lie in the rain shadow formed by the eastern front ranges of the Andes (Cordillera Central and Oriental). The non-riparian vegetation of these areas consists of thorn scrub with mesquite (Prospis), palo verde (Cercidium), and columnar cacti (Cereus and Cephalocereus) dominating. Although this area is adjacent to the lowest part of the Andes in Peru, the xerophyllus vegetation of these valleys is not continuous with that of the coastal area.

On the coastal side of the Andes, most of the species of Tropidurus are restricted to the coastal plain, with only tigris and koepckeorum occurring in the foothills. Three of these species (occipitalis, peruvianus, thoracicus) have wide but ecologically limited distributions. The fourth, theresiae, is locally abundant but appears to have a limited distribution. It is known from a few localities between the Paracas Peninsula and Huacho in or just above the intertidal zone with little
or no vegetation. Its distribution may be limited by the larger, more common *T. peruvianus*. The latter is essentially intertidal, extending just a few hundred meters above the high tide line, where it feeds largely on either marine arthropods or insects which are in turn supported by the washed-up dead and decaying marine plants and animals. The known prey items of *T. thersiae* suggest that they feed near water, if not in it. Most of the localities from which they are known are adjacent to calmer waters of large bays. *Tropidurus thoracicus*, perhaps due to its diet, occurs only in areas with perennial vegetation. It is most common in the riparian communities along the coast but occurs also in the Lomas vegetation of the foothills. *Tropidurus occipitalis* also occurs in areas of permanent vegetation but is distributed from just south of the Sechura Desert north into Ecuador. It is broadly sympatric with *thoracicus* but is insectivorous and more scansional. It is unlikely that it competes directly with *thoracicus*. Both of these species, however, may be in direct competition with species of the genus *Dicrodon* (Teiidae). It is entirely plausible that the presence of large numbers of *Dicrodon gutullatum* (herbivorous) across most of the Sechura Desert contributes to the absence of *thoracicus* in the area. On the other hand, *Dicrodon heterolepis*, an insectivorous species, has a geographic range that largely complements that of *occipitalis*. It ranges from the southern edge of the Sechura Desert south to Ica. Regardless of the causes, the vegetated areas of the coastal plain usually contain only one dominant insectivorous and one dominant herbivorous species of diurnal lizard. Less abundant insectivorous species of other teiid and iguanid genera occur in some of the riparian associations, but are sufficiently rare to have little impact on the coastal communities.

Both *koepckeorum* and *tigris* occur in the rocky habitats of the coastal hills and Andean foothills of coastal Peru. Both are largely scansional species, occurring on rocks, and appear to be ecologically and, to a large extent, morphologically similar. They have complementary geographic ranges, with *koepckeorum* occupying the more heavily vegetated areas of northern Peru. We did not observe the two species in sympathy, but specimens of both bearing the same locality data (Shigiyaj, 1600 m, collected by P. O. Simon) are known, indicating that they may be sympatric.

All of the coastal species were found in sympathy with at least one other species of *Tropidurus* (Table 2). As would be expected, the three wide ranging species occurred more often in sympathy with other species. *Tropidurus peruvianus* is sympatric with *occipitalis* (vicinity of Cancas) and *thoracicus* (vicinity of Culebras) in situations where vegetation is present at the storm tide levels. Otherwise, *peruvianus* occurs only with *theresiae*. In addition to *peruvianus*, *occipitalis* occurs in sympathy with *thoracicus* and *koepckeorum*. In areas of sympathy with *koepckeorum*, the habitat consisted of well-vegetated foothills areas, dominated by boulders, with *Tropidurus koepckeorum* being more abundant. Both species are scansional, with *occipitalis* occurring on the limbs and trunks of trees and shrubs and *koepckeorum* on rocks and boulders. Aside from *occipitalis*, *koepckeorum* was not found in sympathy with other species, but may occur with *tigris*, as discussed above. In addition to its probable sympathy with *peruvianus*
Table 2

Occurrence of sympatry between species of *Tropidurus* on the coast of Peru (x = observed; P = probable, as discussed in text).

<table>
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<tr>
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<th>peruvianus</th>
<th>theresiae</th>
<th>thoracicus</th>
<th>tigris</th>
<th>occipitalis</th>
<th>koepckeorum</th>
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<tbody>
<tr>
<td>peruvianus</td>
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<tr>
<td>theresiae</td>
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<td></td>
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<tr>
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<tr>
<td>tigris</td>
<td>P</td>
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<tr>
<td>occipitalis</td>
<td>X</td>
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<tr>
<td>koepckeorum</td>
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<td>P</td>
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(see *tigris* account), *tigris* was observed in sympatry with *thoracicus* in the foothills northeast of Ica where the perennial vegetation of the valley floors approached boulders scattered along the margin of essentially unvegetated slopes.

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Resumen

Hasta el presente, ocho especies del género *Tropidurus* han sido encontradas en el Perú; representan dos grupos principales de especies. En el grupo *occipitalis*, que abarca *T. occipitalis*, *T. koepckeorum* y *T. stolzmanni*, las escamas dorsolaterales son guilladas, mucronadas e imbricadas; la cresta a lo largo de la mitad del dorso es prominente. Las especies de este grupo son primariamente trepadores. En el grupo *peruvianus*, que abarca *T. peruvianus*, *T. melanopleurus*, *T. theresiae*, *T. thoracicus* y *T. tigris*, las escamas dorsolaterales son lisas, granulares y yuxtapuestas. Las especies de este grupo son primariamente terrestres. Las especies pertenecientes al mismo grupo se diferencian principalmente por el tamaño, la coloración y la disposición de la coloración. *Tropidurus* peruvianus abarca varias razas descritas, dos de las cuales, *T. p. peruvianus* y *T. p. salinicola*, se encuentran en el Perú. Presentamos descripciones de tres razas propuestas de *T. thoracicus*: *T. t. thoracicus*, *T. t. talarae* subespecie nueva, y *T. t. icae* subespecie nueva. Todas las otras especies se consideran monotípicas.

Con la excepción de *T. stolzmanni*, todas las especies peruanas de *Tropidurus* se restringen a habitaciones secas costaneras. *Tropidurus stolzmanni* se encuentra

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