

MISCELLANEOUS PUBLICATIONS  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 56

TAXONOMIC AND GEOGRAPHIC  
COMMENTS ON GUATEMALAN  
SALAMANDERS OF THE  
GENUS *OEDIPUS*

BY  
L. C. STUART

ANN ARBOR  
UNIVERSITY OF MICHIGAN PRESS  
JANUARY 30, 1943

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FREDERICK M. GAIGE  
Director of the Museum of Zoology

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# TAXONOMIC AND GEOGRAPHIC COMMENTS ON GUATEMALAN SALAMANDERS OF THE GENUS *OEDIPUS*<sup>1</sup>

## INTRODUCTION

IN 1936 Schmidt reviewed the species of salamanders known to occur in Guatemala and presented a geographic analysis of their distribution on the volcanoes. His paper correctly allocates all the Guatemalan Oedipi to that date and serves as the basis upon which this study and all future investigations of these amphibians in that area must rest. To Schmidt's list I have added three species described herein as new and have been able to clarify further the status of several others unknown or poorly known to that author.

The following account is divided into two sections. The first part presents an annotated list of the ten species which I collected in Guatemala, and the second is a geographical study—possibly somewhat premature—of the salamanders of Guatemala with particular emphasis on those of the Alta Verapaz.

Including the forms here reported, the Guatemalan salamander fauna consists of twenty species, and at least another four are so close to the country's borders that they may be considered a part of its fauna:

<i>Oedipus bromeliacia</i> Schmidt	<i>Oedipus lincolni</i> , sp. nov.
<i>Oedipus cuchumatanus</i> , sp. nov.	<i>Oedipus mexicanus</i> (Dumeril and Bibron)
<i>Oedipus dofleini</i> (Werner)	<i>Oedipus morio</i> Cope
<i>Oedipus elongatus</i> Schmidt	<i>Oedipus mulleri</i> (Brocchi)
<i>Oedipus engelhardti</i> Schmidt	<i>Oedipus occidentalis</i> (Taylor)
<i>Oedipus flavimembris</i> Schmidt	<i>Oedipus odonnelli</i> , sp. nov.
<i>Oedipus flaviventris</i> Schmidt	<i>Oedipus rex</i> Dunn
<i>Oedipus franklini</i> Schmidt	<i>Oedipus rostratus</i> (Brocchi)
<i>Oedipus goebeli</i> Schmidt	<i>Oedipus rufescens</i> Cope
<i>Oedipus helmrichi</i> Schmidt	<i>Oedipus salvinii</i> Gray

In addition to the above, the following will unquestionably be shown to be a part of the Guatemalan fauna:

<i>Oedipus dunni</i> Schmidt	<i>Oedipus schmidti</i> Dunn
<i>Oedipus nasalis</i> Dunn	<i>Oedipus yucatanus</i> (Peters)

Since the Sierra de las Minas has not been explored and the Sierra de Merendón is barely known, this represents an enormous fauna, and no other area of comparable size possesses such a wealth of Oedipi. As will be explained, the complex makeup of the fundament with isolated mountains,

<sup>1</sup> Because I question the validity of the name *Oedipus* for the orthopteran genus of Berthold, I retain the name of Tschudi for this amphibian group.

sharply demarked physical boundaries, and extremes of climate has undoubtedly been the most important factor in the origin of this fauna.

Although Schmidt found salamanders in almost unbelievable numbers on the volcanoes, my own collecting in Alta Verapaz and in the Sierra de los Cuchumatanes of El Quiché revealed no such condition nor any approach to it. My entire collection of salamanders, assembled during 12 months of field work in 1938 and 1940, numbers only 175 specimens divided among 10 species. In comparison with Schmidt's collection of salamanders from Guatemala, my own collections seem most disappointing. They have, nevertheless, enabled me to clarify the status of several dubious forms, to present a somewhat detailed study of their distribution in a second "biotic area" of Guatemala (Schmidt's study of the volcanoes representing the first), and to give some information on the fauna of the heretofore unexplored Sierra de los Cuchumatanes.

Inasmuch as some of my collections were made at stations which do not appear on any map, a list of these localities is presented below (all distances are measured in a straight line) :

#### Alta Verapaz

- \*Cobán, capital of the province, 15° 28' N., 90° 19' W.<sup>2</sup>
- \*Finca Chejel, 30 km. southeast of Cobán on the Baja Verapaz border (administered from Baja Verapaz).
- \*Finca Chichén, 9 km. south and slightly east of Cobán.
- \*Finca Los Alpes, 35 km. east and slightly south of Cobán.
- Finca Los Pinales, 44 km. east and slightly north of Cobán.
- \*Finca Samac, 6 km. due west of Cobán.
- Finca Santa Teresa, 23 km. southeast of Cobán.
- Finca Volcán, 41 km. east of Cobán.

#### El Quiché

- Nebaj, 15° 25' N., 91° 8' W.
- Salquil Grande, 15 km. west and slightly north of Nebaj (more correctly spelled "Xolquil Grande").

#### ACKNOWLEDGMENTS

For the aid given me and the courtesies shown me in the field, I am indebted to a host of friends, and due acknowledgment will appear in a forthcoming paper summarizing my Guatemalan investigations. For financial aid I wish to acknowledge, at this time, grants from the Baird Endowment Fund and from the Horace H. Rackham School of Graduate Studies, both

<sup>2</sup> An asterisk (\*) indicates that the locality is listed on Sapper's map (1901). Unfortunately, the scale of kilometers on this map is given for latitude 0° and my distances do not agree with those measured by Sapper's scale. The distances cited here are based on a scale of kilometers constructed for use at 15° N.

of the University of Michigan. To my friends K. P. Schmidt, of the Field Museum of Natural History, and E. R. Dunn, of Haverford College, whose knowledge of and experience with the genus *Oedipus* have contributed much to the following comments, I wish to express my thanks for the advice they have so freely placed at my disposal.

ANNOTATED LIST OF SPECIES

*Oedipus lincolni*, new species

(Pl. I, Fig. 1)

TYPE.—An adult male, University of Michigan Museum of Zoology, No. 89107. Collected by L. C. Stuart, July 19, 1940.

TYPE LOCALITY.—*Monte* at Salquil Grande, El Quiché, Guatemala. Altitude, 2450 meters.

DIAGNOSIS.—An *Oedipus* very close to *franklini*, with 13 costal grooves, adpressed legs separated by 2 costal grooves, toes with 2 phalanges free from web, maxilla toothed, teeth piercing lip, vomerine teeth 12–13 in number. Belly dark and a red stripe middorsally from tip of snout to tail. Readily distinguished from *franklini* by its fewer vomerine teeth, shorter legs, and shorter and narrower head in relation to the head-body length.

DESCRIPTION OF HOLOTYPE.—Body robust. Costal grooves 13 in number, the adpressed legs separated by 2 costal grooves. Body length slightly more than 3 times head length (measured to gular fold) and about  $4\frac{1}{3}$  times the head width. The tail is slightly more than  $\frac{3}{4}$  the body length and is slightly constricted at the base. The limbs are well developed, and 2 terminal phalanges of the toes are free from the web. The snout is truncate. The maxilla is toothed, and the upper lip is pierced by the maxillary teeth. There are 12 vomerine teeth on either side forming an arch which extends from behind the choanae medially and posteriorly. A fold behind the eye forms a dermal pocket behind which is a groove extending posteriorly to above the angle of the mouth, where it turns sharply, and then ventrally behind the jaw angle.

The ground color of the preserved specimen is bluish black. The dorsum from the tip of the snout to the base of the tail is occupied by a light brownish yellow stripe in which are 2 dark nape spots and another spot middorsally at the center of the back. The dorsal surface of the tail is flecked with brownish yellow, as are the dark ventral surfaces. The upper surfaces of the arms and legs are mottled with black and yellow. In life the light areas were brick-red.

Total length, 104 mm.; head length, 13 mm.; body length, 44 mm.; tail length, 47 mm.

PARATYPES.—University of Michigan Museum of Zoology, Nos. 89108–9, collected with the holotype.

RANGE.—Although known only from the type locality, further collecting will undoubtedly reveal that this species is widespread throughout the Sierra de los Cuchumatanes.

VARIATION.—Aside from the fact that the holotype is somewhat more slender than are the paratypes, there is no appreciable variation in the 3 specimens at hand.

HABITS.—The types of this species were collected beneath stones in a *milpa* and in the *monte* at Salquil Grande. This area is in the high meadow zone just below the high, wet, cold “temperate forest.” Both *O. rostratus* and *O. rex* were taken in the forest a thousand feet higher, where *lincolni* was apparently not present. The scattered pine and oak in the “high meadows” of the Sierra de los Cuchumatanes suggest that the meadows are the result of human occupancy.

RELATIONSHIPS.—This new form is very close to *O. franklini*, which it resembles in all major morphological features, although *franklini* is a bromeliad form (Schmidt, 1936: 161) and *lincolni* is a ground type. *O. lincolni* has a somewhat greater body length than has *franklini*, and this accounts for its relatively shorter legs and shorter and narrower head.

This species is dedicated to my friend, the late Dr. J. Stewart Lincoln, at whose suggestion I visited the Sierra de los Cuchumatanes and with whom I climbed Cerro Salquil.

### *Oedipus odonnelli*, new species

(Pl. II, Fig. 3)

*Spelerpes mulleri*, Brocchi, 1882: 116 (in part), Pl. XX, Fig. 3.

TYPE.—An adult male, University of Michigan Museum of Zoology, No. 89096. Collected by L. C. Stuart, March 28, 1940.

TYPE LOCALITY.—*Cafetal* just east of the hacienda at Finca Volcán, Alta Verapaz, Guatemala. Altitude, 1200 meters.

DIAGNOSIS.—An *Oedipus* of the *platydactylus-mexicanus* series with 12–13 costal grooves, adpressed legs separated by 3–5 costal grooves, toes fully webbed, maxilla toothed, vomerine teeth about 11–15 in number. Ground color gray-blue above, lighter below, and with a bright yellow, dorso-lateral stripe or series of spots on either side. The typical form is readily distinguished from *mulleri* by its 2 dorsolateral stripes in place of a single stripe and from *mexicanus*, which typically possesses 3 dorsal bands.

DESCRIPTION OF HOLOTYPE.—Body robust. Costal grooves 13 in number, the adpressed legs separated by 4 costal grooves; body length a little more than 3 times the head length and slightly less than 5 times the head width. The tail is equal in length to the head-body length and is slightly constricted at the base. The limbs are well developed, and the toes fully webbed. The webs are indented between the toes to produce a scalloped

outline. The snout is broadly truncate. The maxilla is toothed, and the vomerine teeth, 12 in number, form an arched series extending from the choanal groove posteriorly and almost in contact with the opposite series medially.

The ground color of the preserved specimen is gray-blue above and brownish gray beneath. On either side of the back is a linear series of cream-colored irregular spots extending from the hind part of the head posteriorly to the base of the tail. The palms of the hands and feet are somewhat lighter, and there is evidence of cream-colored spotting on the upper surfaces of the feet. In life the light markings were bright yellow.

Total length, 123 mm.; head length, 15 mm.; body length, 47 mm.; tail length, 61 mm.

PARATYPES.—University of Michigan Museum of Zoology, Nos. 89097–89105 from the same locality as the holotype.

RANGE.—Known only from the type locality, but possibly an inhabitant of the cloud forests of eastern Alta Verapaz.

VARIATION.—The type series of this species indicates that it is remarkably constant. In proportional measurements the body is always slightly more than 3 times as long as the head and is  $4\frac{1}{3}$  to  $5\frac{1}{3}$  times the head width. The tail and head-body lengths are about equal, varying one way or the other but slightly, and the legs fail to overlap by 3 to 5 costal grooves. The teeth number 11 to 15.

The greatest variation in this species exists in its pattern in which, although always basically the same, the light, dorsolateral stripes range from sharply demarked bands to a linear series of separated spots. The extent of these bands on the tail is also variable, but always appears as a series of spots rather than a continuous stripe.

HABITS.—I found this species only beneath the leaf sheaths of bananas at the base of the cloud forest. Although I did not collect it in the cloud forest proper, where animal life is relatively scarce, the absence of the form from lower altitudes, which I collected thoroughly, may be taken as an indication that it represents a cloud forest inhabitant.

TAXONOMIC NOTES.—So far as I know, no positive mention of this species has been made in the literature. It is, however, entirely possible that some of the European museums (especially German) may possess specimens received from the Alta Verapaz and catalogued under the name of *mulleri*, *platydactylus*, *mexicanus*, or *variegatus*. The closest approach in the literature is Brocchi's (1883: 116, Pl. XX, Fig. 3) comment on and figure of a specimen from the Río Polochic. This specimen has the two lateral stripes of *odonnelli* and, in addition, a very narrow middorsal, light stripe. This undoubtedly represents a *mexicanus-odonnelli* intergrade.

It may be possible to confuse this species with certain specimens of *mexi-*

*canus*. I have, in fact, examined a specimen from Cofradía, Honduras, in the collections of the American Museum of Natural History, which, instead of possessing the 3 irregular, dorsal, light stripes of *mexicanus*, corresponds very closely to *odonnelli* in that it has only 2 dorsal, light stripes. Nevertheless, these 2 stripes are extremely irregular in outline rather than cleanly delimited as in *odonnelli*, and the belly is, as is characteristic of *mexicanus*, much less heavily pigmented.

RELATIONSHIPS.—The relationships of the *platydactylus* group of *Oedipus* will be discussed under *O. mulleri*. The species most nearly related to *odonnelli* appear to be *mulleri*, living directly to the west in the highlands of the Alta Verapaz, and the lowland *mexicanus*. There is little reason to suspect *odonnelli-mulleri* intergradation, but *odonnelli-mexicanus* intergrades, such as the specimen figured by Brocchi, are known. At Finca Los Alpes I collected a similar specimen (No. 89106) at 600 meters altitude. In this and in the one figured by Brocchi the middorsal stripe of *mexicanus* is greatly reduced, but is still evident. The occurrence of both at lower altitudes is, of course, in keeping with the expectation of intergradation between the lowland *mexicanus* and upland *odonnelli*. Intergradation is also to be looked for on the northern slope of the Alta Verapaz facing the Petén.

To my host at Finca Volcán, Mr. Reginald O'Donnell, who first described this species to me, I have the pleasure of dedicating this salamander.

*Oedipus mulleri* (Brocchi)

(Pl. II, Fig. 4)

*Spelerpes mulleri*, Brocchi, 1882: 116 (in part), Pl. XX, Figs. 4-5 (type locality, several localities in "haute Vera Paz," here restricted to "les montagnes qui dominant Coban").

Finca Samac, Nos. 89127-30.<sup>3</sup>

DIAGNOSIS.—An *Oedipus* of the *platydactylus-mexicanus* series with 13 costal grooves, adpressed legs separated by 4 or 5 costal grooves, toes fully webbed, maxilla toothed, vomerine teeth about 11 to 13 in number. Ground color gray-blue above and beneath. There is a moderately broad, yellow, middorsal stripe which extends on the tail. The top of the head, hands, and feet are flecked with yellow.

DESCRIPTION.—Body robust. The 2 males and 2 females before me all possess 13 costal grooves. The adpressed legs are separated by 4 to 5 costal grooves. The body length is  $3\frac{1}{3}$  to  $3\frac{2}{3}$  times as long as the head and  $4\frac{1}{2}$  to  $5\frac{1}{4}$  times the head width. The tail is slightly less than to about  $\frac{1}{3}$  greater than the head-body length and is constricted at its base. The limbs are well developed and stout, and the toes are fully webbed. This web is indented between the toes to produce a scalloped outline of the foot. The snout is

<sup>3</sup> All numbers, unless otherwise specified, refer to specimens in the collections of the University of Michigan Museum of Zoology.

broadly truncate. The maxilla is toothed, and the 10 to 13 vomerine teeth are arranged in a regular and slightly arched series.

The preserved specimens have a gray-blue ground color over their entire bodies. From the orbit on either side is a definite yellowish line or an indication of one that extends backward on the neck, where the lines unite to form a moderately broad, pale yellow, dorsal band which continues on the tail and breaks up into spots that disappear before the tip is reached. The feet and palms are marbled with yellow. In my field journal I noted that in life the dorsal stripe appears as faded yellow on a black background.

Maximum size, a female 146 mm. total length.

RANGE.—Probably restricted to the highlands of western Alta Verapaz.

HABITS.—Although Brocchi stated (1882: 116) that Bocourt found this species living beneath stones near depressions which became ponds in the rainy season and although its body form and size are suggestive of a terrestrial life, I found this species only in bromeliads on trees, and Schmidt (1936: 151) inferred a similar observation. Since Finca Samac lies on the common border of the pine zone and broadleaf cloud forest, I am unable to say which is the preferred habitat, but since extensive collecting in the cloud forest above Finca Samac failed to reveal it, I am of the opinion that it is an inhabitant of the upland pine zone of western Alta Verapaz.

TAXONOMIC NOTES.—Dunn (1926: 402-4) was well aware of the occurrence of variant populations in *platydactylus*, but he lacked sufficient material to enable him to understand the taxonomic significance of these variants. Schmidt (1936: 146-47) was finally able to separate the Guatemalan *mexicanus* and *mulleri* as distinct forms, and he suggested their relationship to *platydactylus* of Mexico and *salvinii* and *flaviventris* of the Pacific littoral. Much of the confusion existing in *mulleri* may be laid to Brocchi's original description, in which he definitely included three separate species, *mulleri*, an *odonnelli-mexicanus* intergrade (previously discussed), and *dofleini* (noted below). In discussing *mulleri*, Dunn (1926: 402-3) erroneously allocated to *mulleri* specimens of *mexicanus* from British Honduras.

Although it does not enter this problem, I take this opportunity to call attention to a confusing error in Taylor's recent paper. He included (1938: 297) in his synonymy of *O. platydactylus*, *Spelerpes punctatum* of Brocchi, and cited the type locality as "Alta Vera Paz, Guatemala." He also cited Plate 20, Figures 3, 4, and 5, of Brocchi (1882) as illustrations of *punctatum*. The type locality of *punctatum* is given as "Mexique" by Brocchi (1882: 115), and the figures to which Taylor refers are definitely labeled "*Spelerpes mulleri*."

RELATIONSHIPS.—Although there is some question as to the position of *salvinii* and *flaviventris*, which Schmidt (1936: 146-47) suggested are offshoots of *platydactylus*, there is little question but that *mulleri*, *odonnelli*,

*mexicanus*, and *platydactylus* (Dunn [in a letter] has suggested *lignicolor* as well) form a compact group. In morphology all are extremely close, and their patterns are readily derived one from the other, as shown in Plate II, Figures 1-4.

*O. platydactylus* is a lowland form with a simple pattern consisting of a broad, yellow or orange dorsal band. To the south and east of this Mexican species exists *mexicanus*, also a lowland type, in which the dorsal light stripe is typically broken by 2, included, longitudinal, somewhat broken, dark stripes. This produces a pattern of 3 rather narrow dorsal bands, 1 mid-dorsally and 1 dorsolaterally on either side.

As *mexicanus* invaded the highlands of the Alta Verapaz, it is indicated that the pattern simplified itself in 2 ways. In the east the middorsal light stripe was gradually darkened to leave a pattern of a light dorsolateral stripe on either side. This is the pattern of *odonnelli*, and the obliteration of the middorsal stripe is indicated by the remnants which still persist in *odonnelli-mexicanus* intergrades. In the west the dorsolateral light stripes of *mexicanus* were obliterated to leave the narrow middorsal stripe of *mulleri*. It may be argued that *mulleri* developed directly from *platydactylus* through a narrowing of the dorsal light coloration, but the tristripped intervening *mexicanus* argues against this. Paralleling this change in the dorsal pattern is an increase in the pigmentation of the ventral surface from *platydactylus* to *mulleri* and *odonnelli*.

Neither *salvini* nor *flaviventris* are thoroughly understood, but their relationships to *platydactylus*, noted by Schmidt (1936: 146-47), are certainly indicated in morphological features and in that their pattern has paralleled, to some extent, that of *odonnelli*. Schmidt's figure of *salvini* (1936: Fig. 17), in fact, might well be taken for a figure of *odonnelli*.

### *Oedipus cuchumatanus*, new species

(Pl. I, Fig. 2)

TYPE.—An adult male, University of Michigan Museum of Zoology, No. 89110. Collected by L. C. Stuart, July 12, 1940.

TYPE LOCALITY.—Oak forest about 2 kilometers north of Nebaj, El Quiché, Guatemala.

DIAGNOSIS.—An *Oedipus* possibly close to *helmrichi*, with 12-13 costal grooves, adpressed legs separated by not more than 2 costal grooves, toes fully webbed, maxilla toothed, vomerine teeth 9-10 in number. Dorsal color mottled purplish brown and reddish brown with a light brown dorsolateral stripe on either side from the eye to the groin. Undersurfaces light. Readily distinguished from *helmrichi* by the more extensive webbing on toes.

DESCRIPTION OF HOLOTYPE.—Normal body form. Costal grooves 12 in number, the adpressed legs almost touching; toes fully webbed, but the web indented between toes to give appearance of an almost free terminal



phalange. Body length about  $2\frac{1}{2}$  times the head length to the gular fold and slightly more than 4 times the head width; tail slightly shorter than the head and body and slightly constricted at its base. The snout is broadly truncate. Maxilla toothed; vomerine teeth in 2 arched series, about 10 in number on either side.

The surface of the head is mottled purplish brown and light reddish brown. This color extends posteriorly to the base of the tail, thus forming a broad middorsal stripe. Laterally, on either side is a narrower, light reddish brown stripe extending from the eye to the base of the tail. The sides are gray-brown, which grades into the light color of the ventrum. The upper surfaces of the tail and of the legs are mottled with purple and reddish brown. The undersurfaces of the head and body are pale yellow, and the tail is light orange-yellow mottled with gray. The reddish brown is more pinkish in life.

Total length, 82 mm.; head length, 12 mm.; body length, 31 mm.; tail length, 39 mm.

PARATYPES.—University of Michigan Museum of Zoology, Nos. 89111-13, collected in the same locality as the holotype.

RANGE.—Known only from the type locality, but possibly widely distributed throughout the Cuchumatán region of Guatemala in the moderately high oak-pine zones.

VARIATION.—In the 3 paratypes there is practically no variation, and in morphological characters they are almost identical with the holotype. In 2 of the specimens, smaller than the holotype, the lateral stripes from the eye to the tail are prominent and sharply demarked; in the third specimen these stripes are absent, and one sees only a dark middorsal region which laterally fades into the ventral coloration.

HABITS.—Of the type series, 3 specimens were found living in bromeliads well above the ground, and the fourth was taken from beneath a log on the forest floor. All were secured in an oak forest mixed with some pine, and the 4 specimens, representing 2 days devoted exclusively to a search for salamanders, are an indication of the rarity of the species. No other salamanders were observed in the oak-pine region that dominates the Nebaj Valley.

RELATIONSHIPS.—A full account of the relationships of this species will be included in the discussion of *O. helmrichi*. It is sufficient to note at this point that *O. cuchumatanus* is, apparently, a connecting link between *O. engelhardti* of the volcanoes and *O. helmrichi* of the Alta Verapaz.

#### *Oedipus helmrichi* Schmidt

*Oedipus helmrichi*, Schmidt, 1936: 152, Fig. 18 (type locality, "mountains above Finca Samac, west of Cobán, Alta Verapaz, Guatemala, at 5000 feet altitude").

Finca Chichén, Nos. 89132-34, 89135 (2).

Finca Samac, No. 89136 (2) topotypes, No. 89137 (12), No. 89138 (5).  
Finca Volcán, No. 89131.

At no place in the Alta Verapaz did I find this recently described species in any abundance. My 25 specimens from widely separated localities show little variation and follow the type description closely in all details. It may be noted, however, that whereas Schmidt records but 6 vomerine teeth in the holotype, I count from 10 to 15 in my series. As noted in the original description, considerable variation exists in coloration, but the variations may all be expressed as minor departures from a basic pattern.

This pattern consists primarily of a broad dorsal band bordered laterally by a dark streak extending from the eye to the groin. Ventrally this dark streak is not sharply delimited, but diffuses gradually into the unpigmented belly. The dorsal light stripe is darkened middorsally in varying degrees to produce most of the pattern variations. In some instances it is very dark middorsally, producing a pattern of a light dorsolateral stripe on either side, in other examples the darkening is so slight that the entire dorsal surface has only the broad, light band. Occasionally, this stripe may be punctated with dark spots. The upper surface of the tail is colored as is the middorsal region of the body. The undersurface of the tail is clear yellow to orange, occasionally carrying a few, scattered, dark spots.

This species is definitely a bromeliad inhabitant, although in many places it occurs beneath the leaf sheaths of bananas. I have never seen it on the ground. At Finca Chichén and Finca Volcán I found it only in the cloud forest above 1400 meters altitude, and it apparently did not descend into the coffee zone despite an abundance of banana plants. At Finca Samac it descended into the pine zone to about 1300 meters, where it was in banana plants. Schmidt (1936: 154) inferred that *helmrichi* lives only at higher levels than does *rufescens*. In the main, I concur with this conclusion, for I have never taken *rufescens* in the cloud forest above the coffee zone, but at Finca Samac the two occurred in the same *cafetales* and frequently in the same banana plant.

In his description of *helmrichi*, Schmidt (1936: 154) was unable to fix its relationships. Fortunately, my discovery of *cuchumatanus* at similar altitudes in the Sierra de los Cuchumatanes to the west clarifies the position of *helmrichi*. It is my opinion that these species, together with the cloud forest *engelhardti*, form a species group.<sup>4</sup> All agree in the amount of webbing on the feet, in possessing an unpigmented ventral surface of the tail (very slightly spotted in *cuchumatanus*), in habitat, in size, and in body proportions. It is wholly possible that *dunni* of the cloud forest of the Sierra de Merendón may fit into this scheme, and should this be true, it is

<sup>4</sup> Taylor (1941: 150) has described *Bolitoglossa nigroflavescens* from Chiapas and has suggested its relationship to *engelhardti*, thus adding a fourth species to this group.

not unreasonable to anticipate the discovery of an undescribed species in the Sierra de las Minas. It is indicated that there exists in Guatemala a compact group of bromeliad *Oedipi* which have differentiated in the cloud forests of the several biotic areas. Just what the relationships of such a group would be to the *rostratus* group, which is very similar in morphological characters but occupies the cypress forests at higher altitudes, is a question that only future field investigations can settle.

It should be noted that Brocchi's record (1882: 113) of *morio* from the Alta Verapaz was unquestionably based upon specimens of *helmrichi*.

*Oedipus dofleini* (Werner)

(Pl. I, Fig. 3)

*Spelerpes dofleini*, Werner, 1903: 352 (type locality, "Guatemala" [presumably the Alta Verapaz<sup>5</sup>]).

Finca Volcán, Nos. 89119-25.

DIAGNOSIS.—An *Oedipus* closely related to *yucatanus*, with 13 costal grooves, 2 or 3 costal grooves separating the adpressed legs, toes fully webbed, maxilla toothed, vomerine teeth irregular. Ground color gray-brown to bluish, marbled or streaked with brown; belly pigmented. Differs from *yucatanus* in possessing longer legs.

DESCRIPTION.—Body robust. All the specimens before me, 2 males and 5 females, possess 13 costal grooves. The adpressed legs are separated by 2 to 3 costal grooves. The body length is 3 to  $3\frac{1}{2}$  times the head length and 4 times, slightly more or less, the head width. The tail, which is constricted at its base, varies from  $\frac{2}{3}$  the head-body length in a juvenile to  $\frac{1}{10}$  the same measurement in a large adult. The limbs are well developed, and the toes are fully webbed. The web is slightly indented between each digit to produce a scalloped outline on the feet. The snout is truncate. The maxilla is toothed, and the vomerine teeth form irregular patches or an uneven series about 12 in number and extend from the choanal groove medioposteriorly, almost in contact with the parasphenoid tooth patches.

In preserved specimens the dorsal ground color is dark gray-blue. In the lightest specimen the top of the head is marbled with light brown, and there is a very irregular streak of the same color dorsolaterally on either side. These streaks are obscured in the darker specimens, and the dorsal surface is irregularly marbled or flecked with brown. There is an indication of brown blotches in the axillary and groin regions and dorsally at the constriction of the tail. The dorsal marbling fades laterally into the gray-blue ground color of the ventrum, which is lighter than the dorsum. The entire under-

<sup>5</sup> Sapper spent much of his time collecting data and traveling in the Alta Verapaz, and since the localities Campur and Cobán are frequently given as collecting localities in Werner's paper, one may logically assume that this species was secured in the same region. Schmidt (1936: 151) seemed positive on this score.

surfaces are uniformly colored or at most lightly flecked with brown. One specimen has small, dark, round spots scattered over the belly and sides. The legs are gray-blue mottled with brown.

In my field journal I have noted that the dorsum was mottled gray and black, the sides were gray and brown, and the undersurfaces uniformly dark gray. The axilla and groin patches were conspicuous and brown.

Maximum size, a female 182 mm. total length.

RANGE.—Although I secured this species at but one station, it is probably generally distributed throughout the Alta Verapaz below the cloud forest.

HABITS.—This form is extremely sluggish and reminds one of the large *Ambystoma* of the United States. It is apparently a ground form and was discovered beneath the piles of rotting vegetation in the *cafetales* at elevations of 700 to 900 meters. It was never found in bromeliads or beneath the leaf sheaths of bananas, where *rufescens* and *odonnelli* were common.

TAXONOMIC NOTES.—Dunn (1926: 415) stated: "Werner's *dofleini* is unquestionably *yucatanus*." Schmidt (1936: 147), on the other hand, suggested that the species be provisionally placed in the synonymy of *O. mexicanus* (Duméril and Bibron). His conclusion was based on the fact that it was geographically remote from *yucatanus* and could not be *mulleri* inasmuch as the two were described from the same type locality (i.e., the Alta Verapaz).

As has been indicated *mulleri* is a part of the *platydactylus-mexicanus* group, and Schmidt was, therefore, correct in considering *mulleri* and *dofleini* distinct, but, knowing the former only through a fragmented specimen (1936: 151), he failed to appreciate the *mulleri-mexicanus* relationship. Dunn allocated *dofleini* to its correct taxonomic position, but, lacking specimens, did not realize its distinctiveness.

It is possible that the type of *dofleini* may be an aberrant or poorly preserved *mulleri*, in which case the above specimens would represent an undescribed form, but Werner's comment (1903: 352), "Nahe verwandt der vorigen Art [*S. variegatus* = *mulleri*], aber viel plumper und robuster . . ." in comparing the above specimens with those of *mulleri* suggests otherwise. Furthermore, his color description (1903: 352), "Färbung graubraun, unregelmässig gelblich weiss gefleckt und gewölkt," is certainly far less applicable to either *mulleri* or the closely associated *odonnelli*. Finally, 4 of my specimens exceed Werner's measurement of 150 mm. for the type of *dofleini*, whereas none of my 14 specimens of *mulleri* and *odonnelli* measures 150 mm., and, with the exception of 1, they are all well below that figure.

There is a bare possibility that the poorly preserved specimen which Brocchi (1882: 116-17) had from the Río de la Pasion in the Alta Verapaz was a specimen of *dofleini* rather than of *mulleri*, to which he allocated it. Dunn (1926: 413, 415) was of a similar opinion, although he placed it with *yucatanus*, to which he also relegated *dofleini*.

RELATIONSHIPS.—The name of the above specimens may be open to discussion, but there can be no question as to their relationships. On the basis of color, the irregular nature of the vomerine teeth, and geographic position, this species is directly related to *yucatanus*.

*Oedipus elongatus* Schmidt

*Oedipus elongatus*, Schmidt, 1936: 165 (type locality, "Escobas, the site of the water supply for Puerto Barrios, Izabal, Guatemala").

Finca Volcán, No. 89126.

The above specimen, a female, coincides in most particulars with the type description. It differs, however, in possessing proportionally shorter head and legs. These differences may well be due to its greater size, since its head-body length is 66 mm. as compared with 41 mm. in the type.

I found this specimen beneath rotting vegetation in a *cafetal* at 700 meters altitude. The species is apparently a ground form restricted to the Caribbean lowlands. *O. elongatus* is one of the numerous representatives of the Caribbean fauna which have invaded the Alta Verapaz from the east by way of the Pochic and Cahabón valleys. Schmidt (1941: 481) recorded a fine series of this species from British Honduras.

*Oedipus rex* Dunn

*Oedipus rex*, Dunn, 1921: 143 (type locality, "Sierra Santa Elena [near Teepam], Guatemala [altitude, 9500 feet]").

Salquil Grande, Nos. 89114–15.

It is with some hesitancy that the above specimens are referred to this species rather than described as new. When compared with a small series of topotypic material the specimens appear to be much more robust and possess comparatively shorter legs. In view of the fact that my material is scanty and that the specimens were associated with *rostratus* in a typical *rex* habitat, it seems best to allocate them to *rex* until more data is forthcoming.

These specimens were collected in the very high cloud forest above Salquil Grande (on Cerro Salquil) at about 3000 meters altitude, beneath a log on the forest floor. In the same area *rostratus* was fairly abundant. The scarcity of *rex* in this locality does not coincide with Schmidt's inference (1936: 156) that on Cerro Santa Elena *rex* and *rostratus* occur in about equal numbers.

*Oedipus rostratus* (Brocchi)

*Spelerpes rostratus*, Brocchi, 1883: 112 (type locality, "Les hauteurs de Tonicapam [Tontonicapam] [Guatemala occidental]").

Salquil Grande, Nos. 89116 (5), 89117 (4), 89118 (4).

I can find no differences between these specimens and a series from Cerro Santa Elena upon which Schmidt has already reported (1936: 155–56).

This species was relatively abundant in the same locality in which *rex* occurred in much smaller numbers. With the exception of 4 specimens from a bromeliad on a partly fallen tree, all were taken from beneath logs on the ground in the high cloud forest (altitude, 3000 meters) on Cerro Salquil.

*Oedipus rufescens* Cope

*Oedipus rufescens*, Cope, 1869: 104 (type locality, "Vera Cruz, Mexico . . . Orizaba, Mexico").

Finca Chejel, Nos. 89151, 89156 (13).

Finca Los Alpes, Nos. 89144 (9), 89145 (16), 89146 (9).

Finca Los Pinales, No. 89142 (3).

Finca Samac, Nos. 89139 (2), 89140 (5).

Finca Santa Teresa, No. 89143 (3).

Finca Volcán, Nos. 89141 (16), 89147-50, 89152 (8), 89153 (5), 89154 (4), 89155 (4), 89157 (2).

Specimens of this widely distributed lowland *Oedipus* were by far the most abundant of any of the species taken in the Alta Verapaz. On the basis of the above series and a large collection from Vera Cruz, Mexico, it is indicated that once all available material is assembled, several geographic races will be recognized. Certainly, the Mexican and Verapaz specimens have some differences, but I do not feel that recognition of these variant populations is warranted at this time. In general, the Verapaz specimens appear to attain a somewhat greater adult size, possess slightly longer tails, and are less robust than are the Mexican specimens. Although variation in pattern is considerable and usually parallel in both series, the Vera Cruz specimens possess a greater amount of ventral pigmentation.

In Alta Verapaz this species is apparently a bromeliad form which with *helmrichi* has taken over the banana habitat, where it occurs in abundance beneath the leaf sheaths. All available records of this form indicate that it is a lowland type. I have never seen it in the cloud forest, although it occurred abundantly in *cafetales* at the cloud forest base at Finca Volcán. Indeed, 1400 meters seems to mark its upper limits. Schmidt (1936: 151) recorded it from almost at sea level, but I have never secured it on the lowlands proper ("banana zone"). My lowest record is for Finca los Panales at about 600 meters. My experience indicates that it reaches its greatest abundance in the "coffee zone" (700-1400 meters).

THE DISTRIBUTION OF THE GUATEMALAN SALAMANDRINE FAUNAS

If one disregards structural and stratigraphic relationships, Guatemala may be looked upon as an intricately folded and eroded highland mass resting upon a broad lowland base. This highland mass may be broken down into four major regions. A high plateau, with a northwest-southeast trend,

extends along the Pacific third of the country and dips from the Mexican border on the north to El Salvador and Honduras on the south and east. Its Pacific face descends in a sharp escarpment to the littoral, and it is bordered on this edge by a continuous line of volcanoes. The plateau is covered for the most part by volcanic deposits, and it is surmounted by irregularly grouped nonvolcanic ranges.

From the plateau three long fingers of mountains extend eastward on the Caribbean littoral. In the north is the calcareous, east-west Cuchumatán-Alta Verapaz complex of mountains. Farther south are the narrower but more massive Chuacús-Minas-Mico series, and along the Honduran border, with a northeast-southwest trend, lies the relatively low Sierra de Merendón. These three masses are separated one from another by two valleys. The Cuchumatán-Verapaz ranges are isolated from the Minas complex, except for a low connecting bridge between Cobán and Salamá, by the valley of the Río Negro on the west and by the Ríos Panimá and Polochic in the east, and the deep cut of the Río Motagua separates the Minas and Merendón ranges. The Cuchumatán and Verapaz elements are, moreover, not continuous, for the gorge of the Río Negro, extending from south to north, divides this northern range.

As previously noted these highland masses rest on a lowland base. On the south and west is the Pacific littoral, broad toward Mexico but narrowing toward El Salvador; the north and east are bounded by the extensive plains of the Petén and the much smaller lowlands of Lake Yzabal and of the lower Motagua Valley.

Inasmuch as Guatemala lies entirely within the tropics, with a latitudinal extent of less than five degrees, the climate is determined primarily by altitudinal variations in temperature and the modifying influences of the physiographic structure on the trade winds. In general, three vertical temperature belts are recognizable, a *tierra caliente* or "tropical zone," a *tierra templada* or "subtropical zone," and a *tierra fria* or "temperate zone." The limits of these three temperature zones are at best very indefinite and vary in extent with respect to the main interest of the various investigators. Sapper (1932: 12) is the only author to have treated temperature *per se*. Griscom (1932), Schmidt (1936), and Dickey and Van Rossem (1938) have all interpreted the various zones in the light of flora and fauna, in addition to climatic values. This has, naturally enough, resulted in much confusion, yet it cannot lessen the reality of the existence of definite temperature zones.

Despite the various names and limits which have been applied to the zones, there is a general consensus of opinion that a temperature break of major importance occurs at the upper limits of coffee cultivation, at which condensation of moisture-bearing winds produces the base of the so-called

“cloud forest.” Such conditions occur in Guatemala at about 1500 meters altitude, where the mean annual temperature roughly approaches 18° C.

As one travels on the plateau of Guatemala and crosses the high ranges which surmount it, another temperature belt becomes apparent. Here again authors are more or less agreed upon a definite break at about 3000 meters altitude. In this region a secondary condensation of moisture in the air produces a very damp and cold forest, which is predominantly cypress. This represents the base of the “temperate zone” and coincides roughly with the mean annual isotherm of 10° C.

There are, then, three temperature belts in Guatemala, a “tropical zone” between 0–1500 meters, a “subtropical zone” between 1500–3000 meters, and a “temperate zone” above 3000 meters. On the highest volcanoes a fourth belt, the “paramo zone” is also recognizable, but it is too limited in extent to warrant treatment. It lies above 4000 meters (*vide* Schmidt, 1936: Fig. 15).

The distribution of precipitation in Guatemala, dependent primarily upon the trade winds, finds its greatest modifying influence in the most northerly mountain range (i.e., the Cuchumatán-Verapaz complex). This range is sufficiently high to block effectively most of the moisture-bearing winds from the southern and western parts of the republic. Inasmuch as the three main mountain masses become lower in the east and swing slightly northward, the trades are able to invade the Polochic and lower Motagua valleys, but the Sierra de las Minas forms a second barrier, which produces rain-shadow conditions in all the area lying to the south.

Guatemala has, then, an extremely humid Caribbean littoral that becomes more humid on the northern faces of the three mountain masses in the east; the remainder of this country, with the exception of the Pacific littoral, the Pacific slopes of the volcanoes, and local areas of “temperate zone,” has varying degrees of aridity, depending upon the precipitation-evaporation index correlated with temperature, which, as has been shown, is determined by altitude. The low middle Motagua Valley, for instance, is desert, the plateau presents an intermediate condition, and the crests of the mountains above the plateau are humid as a result of low temperatures that cause further condensation in the upper air. The Pacific littoral, which might normally be extremely arid, is sufficiently extensive to produce convection currents which deposit some moisture.

If the edaphic influences which modify the vegetation locally (as in the lower Cahabón Valley in the Alta Verapaz) are disregarded the distributional pattern of the vegetation coincides closely with the climate as roughly outlined above. The Caribbean lowlands are clothed in a typical monsoon forest, which, along the face of the Cuchumatán-Verapaz mountain complex, becomes almost true selva as a result of increased precipitation. This low-



land forest extends upward to the base of the "subtropical zone" and may be divided into two separate subzones, the "banana zone" (= *corozo* zone) below 600 meters and the "coffee zone" between 600 and about 1500 meters. This tropical zone occurs also on the Pacific littoral, where the conditions are more arid and where a savanna-forest mixture predominates. As noted by Schmidt (1936: Fig. 15) this Pacific coast tropical area is likewise readily divisible into a lower banana zone and an upper coffee zone. The only other lowland area of any extent in the country is the middle and upper Río Motagua Valley, in which rain-shadow conditions produce extensive desert areas.

The so-called "subtropical zone," extending from approximately 1500 meters to about 3000 meters, because of its extent over the complex physiographic areas already noted, presents a most confusing distributional pattern of vegetation. On the north face of three main mountain masses this region is dominated by cloud forest, which also occurs on the western face of the volcanoes. This cloud forest is extremely humid and may, as Schmidt pointed out (1936: Fig. 15), be subdivided into several categories. Over the rest of the republic, however, rain-shadow conditions prevail, and pine is the dominant vegetational type. The entire plateau and the southern slopes of the mountain ranges, except the Sierra de Merendón, support pine or oak. Local variations occur, however, in such areas as the southeastern end of the plateau, where savanna is dominant as a result of the higher temperature of the lower altitudes and the decreased rainfall, and in the arid interior basins lying between the Cuchumatán-Verapaz and Chuacús ranges, where desert conditions prevail.

The temperate zone is extremely local, occurring only on the volcanoes, the crests of the nonvolcanic mountains above the plateau, and in the Sierra de los Cuchumatanes. As previously noted, the lowered temperature here results in condensation and a very cold wet forest in which cypress is dominant. This region lies above 3000 meters and on the very highest volcanoes (Tajumulco) shades gradually into the treeless "paramo zone."

From the foregoing, it is evident that the distributional pattern of any animal group in Guatemala must be complex. Although Griscom (1932) has attempted to state avian distribution in Guatemala in terms of the "life zone" hypothesis, I do not believe that his data support it, and, certainly, salamandrine distribution does not follow the simple "life zone" arrangement in the country as a whole. In fact, Griscom (1932: 55) noted a lack of coincidence between the subtropical avifauna of the volcanoes and the Alta Verapaz and definitely stated (1932: 64) that his "temperate zone" of the Altos is not a climatic division but, rather, a faunal assemblage. I believe, therefore, that, although employing "life zone" terminology, Griscom actually presented his distributional data in terms of "biotic areas,"

as elaborated by Dice in numerous papers (first statement, 1922). His Caribbean, Pacific, and desert basin faunas lend support to this view.

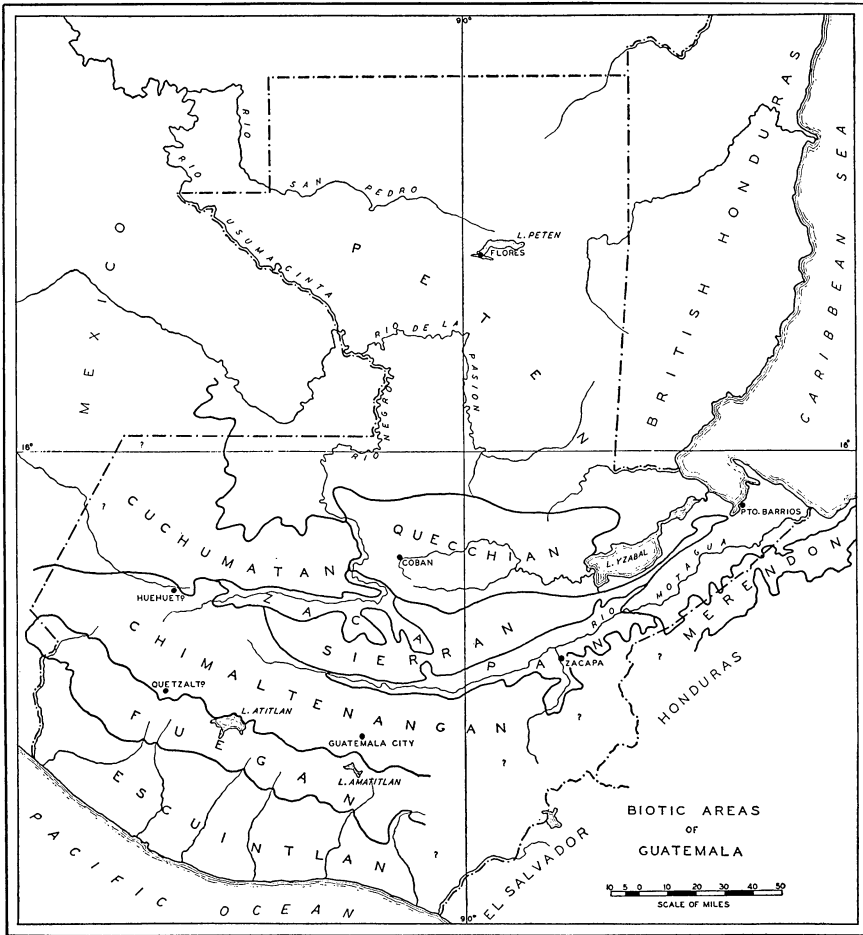
With reference to the salamandrine fauna of Guatemala, the notion of distribution according to "life zone" must also be discarded. Within a single area "life zones" do exist and, in most instances, the fauna arranges itself into such assemblages. Schmidt (1936) has already demonstrated the zonal arrangement of salamanders on the volcanoes. But any attempt to extend a single zone beyond the limits of one "biotic area" is unsuccessful. As a case at point, the cloud forest of the subtropical zone—richest of all zones in salamander species—occurs in four known areas, the Sierra de Merendón, the Sierra de los Cuchumatanes, the volcanoes, and the Alta Verapaz. In this cloud-forest zone eleven species are known to occur, yet not one single species is common to even two of the four areas. The closest approach to any zonal uniformity is in *O. rex*, which is a temperate zone inhabitant of the volcanoes, the Sierra de los Cuchumatanes, and the plateau. There is, however, some suggestion of uniformity running through the various zones. The most outstanding example is the occurrence of the closely related *O. dunni*, *O. engelhardti*, *O. cuchumatanus*, and *O. helmrichi* in the cloud forests of the Sierra de Merendón, the volcanoes, the Sierra de los Cuchumatanes, and the Alta Verapaz, respectively.

Since there is little or no correlation between the salamandrine fauna of Guatemala and the various "life zones," this method of expressing distribution is unsatisfactory. If, however, the salamandrine distribution on the volcanoes is studied, one finds such species as *Oedipus franklini*, *O. engelhardti*, and *O. goebeli* recurring in the subtropical zone on several widely separated mountains. Similarly, on the plateau *O. morio* appears to be generally distributed in the subtropical zone, and *O. rex* and *O. rostratus* occupy the temperate zone. The salamandrine fauna, then, arranges itself into various assemblages in different regions and is distributed zonally within any single region. It is obvious, therefore, that in expressing distribution the "biotic area" concept obtains.

There is a surprisingly close correlation between the distribution of the salamanders and the physiographic (and to some extent climatic and vegetational) provinces included in Guatemala. Although any attempt to so arrange the fauna is at this time premature, I am of the opinion that such an essay is highly desirable, since it may result in an orderly summation of what is now known and may facilitate future investigations. The following arrangement of "biotic areas" in Guatemala is merely an initial survey which, as knowledge increases, will be subject to change and rearrangement.

The definitions of these areas are, moreover, based upon the salamandrine fauna and do not necessarily apply to other groups. Thus, while such groups as the salamanders and terrestrial snails might conceivably show some

parallelism in their distribution, other groups with smaller water requirements might present a different pattern. In a recent paper Schmidt and Stuart (1941) have outlined the "biotic areas" based on the herpetological fauna as a whole. At that time it was suggested that the Sierra de las Minas constituted a wall between two areas, whereas with reference to the sala-



MAP 1

mandrine fauna, there is reason to suspect that this mountain range represents a separate entity.

Yet another factor, which I am unable to consider in my outline, is the relative importance of the various provinces. Although I have considered them all to be on a par, there is reason to suspect that several will eventually be shown to represent only subdivisions or "districts" of more extensive

areas. For the present it seems likely that the Sierra de los Cuchumatanes is a subdivision of the Plateau, and it is wholly conceivable that the Caribbean lowlands in Guatemala are but a minor part of the extensive Central American Caribbean littoral. Any such subdivision must await additional information on adjacent Mexico, El Salvador, and Honduras.

As to the information concerning the various provinces, it will be noted that the volcanoes and the Alta Verapaz are relatively well known, whereas the Sierra de las Minas and the Sierra de Merendón are almost entirely unknown. In the following outline the Alta Verapaz is treated in some detail, because I have been able to investigate this region with some thoroughness.

During my investigations in Guatemala I have been fortunate enough to have visited each of the areas here discussed with the exception of the Sierra de Merendón. As a result I have taken the liberty to interpolate into my outline observations on which no positive evidence exists.

The map of the "biotic areas" is, of course, very provisional. I have not as yet studied Guatemala in sufficient detail to plot the boundaries accurately, and the map has been drawn up primarily at the instigation of my friend, Mr. K. P. Schmidt. The names of the areas (in parentheses) represent nothing more than suggestions.

The following is my concept of the "biotic areas" of Guatemala, based on the salamandrine fauna.

#### PACIFIC LOWLANDS (ESCUINTLAN)

Escuintlan includes the entire Pacific coastal plain and the lower slopes of the escarpment and volcanoes. I am not certain as to whether its upper limit should represent the base of the cloud forest or the base of the "coffee zone." It is characterized by seasonal rainfall and continuously high temperatures. Its vegetation was probably mixed savanna and semideciduous forest, although now it is intensively cultivated and grazed and little virgin country remains. It probably extends from well up in Chiapas, Mexico, to El Salvador. *Oedipus flaviventris* is the only salamander known from the "banana zone" (*vide* Schmidt, 1936), but both *O. salvinii* and *O. occidentalis* occur in the "coffee zone."

#### CARIBBEAN LOWLANDS (PETÉN)

The Caribbean lowlands province practically all lies below 600 meters. Further study may necessitate its division into districts, such as the Petén lowlands and the lower Motagua Valley. Climatically, it is similar to the Pacific lowlands, except that it receives much more rainfall, especially as it approaches the Alta Verapaz highlands. In the north on the plains of the Petén it supports mixed savanna and semideciduous forest, but almost true

selva prevails in the lowlands of the Alta Verapaz and on the Yzabal embayment. It is continuous with the lowlands of Vera Cruz and Tabasco to the north and west and with the drier outer end of the Yucatán Peninsula to the north and is probably faunally distinct from both. It is encroached upon to some extent by the fauna of the Alta Verapaz and, conversely, several of its typical forms invade the latter in the valleys of the Ríos Polochic and Cahabón, so that its boundaries in these areas are indefinite. The salamandrine fauna is:

<i>Oedipus elongatus</i>	<i>Oedipus rufescens</i>
<i>Oedipus mexicanus</i>	<i>Oedipus yucatanus</i> (possibly)

VOLCANOES AND PACIFIC ESCARPMENT (FUEGAN)

This province extends along the entire Pacific side of Guatemala from Mexico into El Salvador. On the west face the volcanoes descend (either to 600 meters or only to 1500 meters, depending upon the upper limit of the Escuintlan) to the Pacific littoral and on the east adjoin the Plateau. Schmidt (1936) has given an excellent account of this province. In the following lists of the salamandrine fauna an asterisk (\*) indicates an endemic species in the Guatemalan parts of the provinces:

Tropical Zone	Subtropical Zone
* <i>Oedipus occidentalis</i>	* <i>Oedipus bromeliacia</i>
* <i>Oedipus salvinii</i>	* <i>Oedipus engelhardti</i>
	* <i>Oedipus flaviventris</i>
Temperate Zone	* <i>Oedipus franklini</i>
<i>Oedipus rex</i>	* <i>Oedipus goebeli</i>

PLATEAU (CHIMALTENANGAN)

The Plateau biotic province is bordered on the west by the volcanoes, on the east it is extremely irregular as a result of entrenchments cut by numerous rivers of the Caribbean watershed. It extends from the south-facing wall of the Sierra de los Cuchumatanes in the north into Honduras in the south. For the most part it lies above 1500 meters, but along the Honduran border it becomes somewhat lower. It is entirely covered with igneous materials and is surmounted by nonvolcanic mountain ranges exceeding 3000 meters altitude. The subtropical sections are semiarid. Human occupation has left little of the original cover, but the greater part of the province was undoubtedly in pine and pine and oak. The lower eastern end very probably contained extensive savanna and pine areas. The crests of the nonvolcanic ranges are temperate and very humid and support pine and cypress forests. The following salamanders are recorded from this province:

Subtropical Zone	Temperate Zone
* <i>Oedipus morio</i>	<i>Oedipus rex</i>
	<i>Oedipus rostratus</i>

## SIERRA DE LOS CUCHUMATANES (CUCHUMATÁN)

Included in this province are the Cuchumatáns proper and several associated minor ranges. This area lies due north of the western end of the Plateau province and is demarked by a high, abrupt wall of schists and serpentine, which lie directly north of the valleys of the upper Ríos Negro and Salegua. The Cuchumatáns proper extend due north from the center of this wall, thus producing an inverted T-shaped highland area. The eastern side of the inverted T is excessively humid as a result of the rising trade winds, and the western side, in the rain-shadow, is somewhat more arid. The eastern slopes extend from the Caribbean lowlands into the temperate zone and, except for a few local areas, are covered with the typical lowland forest, subtropical cloud forest, and the high cold temperate cypress forest. On the west, the northern section represents a continuation of the dry upper Chiapas Valley and at higher altitudes is predominately covered with pine and oak-pine.

I have visited only the eastern side of this province and have not had an opportunity to collect either at lower altitudes or in the cloud forest proper. My collections originated from the local oak-pine region of Nebaj and from the temperate forest above that locality. Further investigations will undoubtedly reveal a fairly rich salamandrine fauna.

From the tropical zone some of the species characteristic of the adjacent Caribbean lowlands may be expected, and the cloud forest may yield forms closely related to the similar belt of the Alta Verapaz. Definitely recorded from this province are the following:

Subtropical Zone	Temperate Zone
* <i>Oedipus cuchumatanus</i>	<i>Oedipus rex</i>
* <i>Oedipus lincolni</i>	<i>Oedipus rostratus</i>

## SIERRA DE LAS MINAS (SIERRAN)

This province includes not only the massive Sierra de las Minas but the Sierra de Chuacús and the Sierra de los Micos, as well. No other province in Guatemala is so poorly known, offers so many difficulties, or promises so much as this mountain mass. The range as a whole is most massive and highest in the west, where it adjoins the plateau; it becomes progressively lower and narrower toward the east. It extends from sea level to more than 3000 meters in altitude, with the northern face of its eastern extension exposed to the moisture-laden trade winds, and with the western extension and entire southern face in a rain-shadow; it offers the most varied conditions to be found in Guatemala.

It has been my good fortune to fly across the arid southern face of the Sierra de las Minas, barely missing the temperate, cloud-enshrouded forests of the crests, and finally, on the northern slopes, winding down narrow

gorges, whose virgin, rain-forested walls were but a few yards from the wing tips. On the single road which crosses this range between Cobán and El Rancho, one leaves the humid forests of the Alta Verapaz, drops into the desert basin of Salamá, and then climbs sharply up through pine and oak to about 1500 meters altitude, where the humid pine forest is rich in moss and epiphytes and numerous mountain brooks make the country rugged indeed. Finally, one descends again to the dry, hot desert of the middle Motagua Valley.

From this entire region not a single reptile or amphibian is known, but anticipating its obvious richness, I look upon it as a separate biotic province. Because of the lack of trails and inhabitants over most of the area, the only points from which it may be investigated are the settlements of isolated families of Indians along the road between San Gerónimo and Morozán.

#### SIERRA DE MERENDÓN (MERENDÓN)

For a knowledge, extremely scarce to be sure, of this range, one is indebted to the investigations of Schmidt (1933). Although no collections have as yet been made on the Guatemalan slopes of the Sierra de Merendón, it does not seem improbable that, because of its northeast-southwest trend, the Honduran and Guatemalan slopes will prove to be similar to one another. The range rises from sea level and extends upward to about 1800 meters (6000 feet), and a typical cloud forest occurs above 1200 meters (4000 feet), according to Schmidt (1933: 15). He further suggested (1936: 144) that this range may be an important center of salamandrine evolution. Three species are at present known from it, and these are from the Honduran slopes:

Tropical Zone  
\* *Oedipus schmidti*

Subtropical Zone  
\* *Oedipus dunnii*  
\* *Oedipus nasalis*

#### INTERIOR DESERT BASINS (ZACAPAN)

This province includes not only the low and very arid valley of the middle and upper Río Motagua but also the higher basins lying between the Sierra de Chuacús and the gorge of the upper Río Negro (Schmidt and Stuart, 1941). The faunal affinities of these latter are still uncertain, but in many respects these valleys are similar to, although isolated from, the Motagua Valley. The high moisture requirements of salamanders eliminate, of course, the possibility of the occurrence of any species of *Oedipus*, and therefore, these areas stand out as a distinct biotic province.

#### ALTA VERAPAZ (QUECCHIAN)

The Alta Verapaz, which represents a highland area of folded limestone in contact with the crystalline Sierra de las Minas on the south, descends to

the lowlands of the Yucatán Peninsula on the north in a series of decreasingly lower ridges. On the west it adjoins the structurally related Sierra de los Cuchumatanes, from which it is separated by the deep gorge of the Río Negro; to the east it dips gently to the Yzabal and Caribbean lowlands.

This highland mass has been deeply eroded by the Polochic-Panimá river system to the south, where it is in contact with the Sierra de las Minas, and the Río Cahabón has cut a deep valley through its central part. This leaves a southern highland area that, for convenience, may be referred to as the Xucaneb division, reaching about 2500 meters altitude, and a somewhat lower mass on the north, the Pocolhá division, which drops gently to the Petén lowlands.

Inasmuch as the altitude of the entire area at no place reaches temperate conditions, only the tropical and subtropical temperature belts are present. The 1200-meter contour line appears to be the boundary between the two. The moisture-laden trade winds sweeping across the Caribbean lowlands rise sharply on the north face of the Pocolhá division, and the rainfall is excessively heavy in that region (more than 5000 mm. in some places), thus producing rain-shadow conditions within the valley of the Río Cahabón. Since the Xucaneb division of the Alta Verapaz (the area to the south of the Río Cahabón) attains a greater altitude than does the Pocolhá division, the northern slope of the higher parts of the Xucaneb mass also receives abundant rainfall. As the area lies behind the relatively high Pocolhá ridge proper to the north, local rain-shadow conditions are evident in the western part. It might be expected that the valley of the Río Polochic would, like that of the Río Cahabón, be dry, since it lies in the rain shadow of the high Xucaneb mass. Such, however, is not the case, except in its upper parts, for local winds bring in moisture from the Yzabal depression. The gorge of the Río Negro to the west of the Polochic Valley receives none of this moisture and is arid.

Despite the fact that almost all of the Alta Verapaz below 1500 meters altitude has been under intensive cultivation since pre-Columbian times, there is sufficient virgin forest left to permit a fairly accurate conception of the original cover. The tropical zone adjacent to the Petén and the north face of the Pocolhá mass are clothed in almost true selva, which on isolated higher areas (above about 1200 meters) becomes "cloud forest." The valley of the Río Cahabón, being in the rain-shadow, is savanna in the east, and in the west in the higher altitudes in the Cobán region, where the rainfall effectivity is greater, pine is dominant. The higher parts of the northern face of the Xucaneb division lie outside the rain-shadow influence, and extensive cloud forests are developed. The lower valley of the Río Polochic, which adjoins the Yzabal lowlands, receives sufficient moisture from local winds to produce a typical monsoon forest; the upper end of the



valley as well as that of the Río Panimá, in the shadow of the Xucaneb ridge proper, is largely pine. The gorge of the Río Negro, also in the rain shadow, is covered with arid pine and savanna.

The complexity of this vegetational pattern would of itself not offer any great difficulties in the correlation of this pattern with the fauna. Unfortunately, the Alta Verapaz has been markedly affected by human occupation. Along the south side of the Cahabón Valley, for instance, from Carchá to above Cahabón there is not a single stand of virgin forest below about 1400 meters. The same condition exists in practically all parts of the province. This circumstance has had a profound effect upon the fauna. With particular reference to salamanders, coffee cultivation has opened up a highway for cloud-forest forms to invade lower altitudes, through the banana plant, which is used for shade. *Oedipus helmrichi* and *O. odonnelli* are striking examples of such an occurrence. Similarly, the clearing of the coffee-zone forests have enabled some of the *monte*-inhabiting lowland types to extend their normal ranges upward.

A second point of confusion arises from the fact that the Caribbean lowlands invade this mountain mass with long tongues stretching up the valley of the Río Negro and the Ríos Polochic and Cahabón. In these regions there is, therefore, a strong admixture of the two faunas. Finally, the complex structure of the Alta Verapaz does not permit the simple zonal arrangement of the fauna, such as occurs on the volcanoes. The province must, rather, be divided into "districts" (Dice and Blossom, 1937: 45) upon which may be superimposed vertical "life belts."

The pine zone in western Alta Verapaz and the savannas of the lower Río Cahabón Valley are clear-cut districts. The broad-leaf forests, on the other hand, occupying the lowlands and the Pocolhá and Xucaneb highland areas have three definite "life belts," the "banana zone" and the "coffee zone," which are tropical, and the subtropical cloud forest. Thus, there are difficulties not only in delimiting the whole but also in describing the distributional patterns within the Alta Verapaz province.

At the outer limits (I am here considering only the salamandrine fauna), its southern boundary is marked by the Sierra de las Minas, as is indicated in the line of weakness occupied by the Panimá-Polochic Valley in the east and the Río Negro gorge in the west. This latter area is not a division of the Alta Verapaz, but of the Interior Desert Basins previously described.

I have never taken any species of the salamandrine fauna in the "banana zone" of the broad-leaf forest. The occurrence of *Oedipus rufescens* and *O. elongatus*, both Alta Verapaz forms, at Escobas in Yzabal (Schmidt [1936: 151, 165]) indicates that my failure to discover them at lower altitudes in this area was very probably the result of faulty field technic. *O. mexicanus* and *O. dofleini* are also to be expected in this zone. The "coffee zone," as I

have suggested, now has a considerable admixture, so that it has a rich fauna. In this zone I have taken *O. rufescens*, *O. dofleini*, and *O. odonnelli* (possibly an invader from the cloud forest), as well as an *odonnelli-mexicanus* intergrade.

I have found only *O. rufescens* in the savanna area of the lower Cahabón, and the relatively arid conditions occurring here seem to preclude any expectancy of other species. In the pine belt of the subtropical zone *O. rufescens*, *O. mulleri*, and *O. helmrichi* all occur, but, as previously indicated, the last named is undoubtedly an invader from the cloud forest. The subtropical cloud forest, where I secured only *O. helmrichi* and *O. odonnelli* on its lower edge, is almost completely restricted to the Xucaneb highland mass.

A list of the salamandrine fauna of the Alta Verapaz is presented in zonal arrangement. The left column indicates the distribution of the fauna as it is definitely known to occur, the right column represents my conception of conditions as they probably existed before human occupation of the area.

Tropical Zone

* <i>Oedipus dofleini</i> <i>Oedipus elongatus</i> <i>Oedipus mexicanus</i> (probably)	* <i>Oedipus dofleini</i> <i>Oedipus elongatus</i> <i>Oedipus mexicanus</i> <i>Oedipus rufescens</i>
* <i>Oedipus odonnelli</i> <i>Oedipus rufescens</i>	

Subtropical Zone

* <i>Oedipus mulleri</i> <i>Oedipus rufescens</i>	* <i>Oedipus helmrichi</i> * <i>Oedipus mulleri</i> * <i>Oedipus odonnelli</i>
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L. C. STUART

PLATE I

- FIG. 1.—*Oedipus lincolni*, holotype, No. 89107, slightly enlarged.  
FIG. 2.—*Oedipus cuchumatanus*, holotype, No. 89110,  $\times 1\frac{1}{2}$ .  
FIG. 3.—*Oedipus dofeini*, No. 89119,  $\times \frac{3}{4}$ .

PLATE I

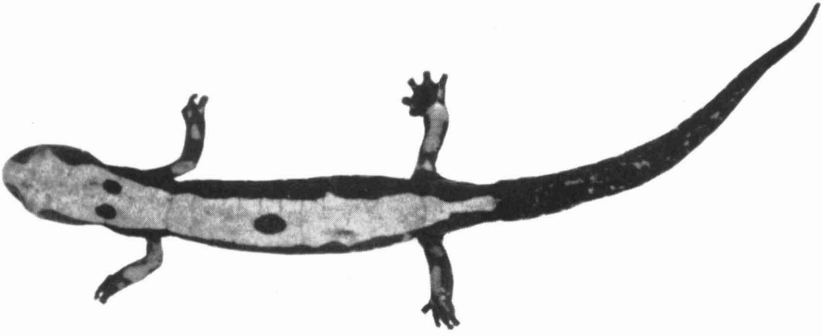


FIG. 1

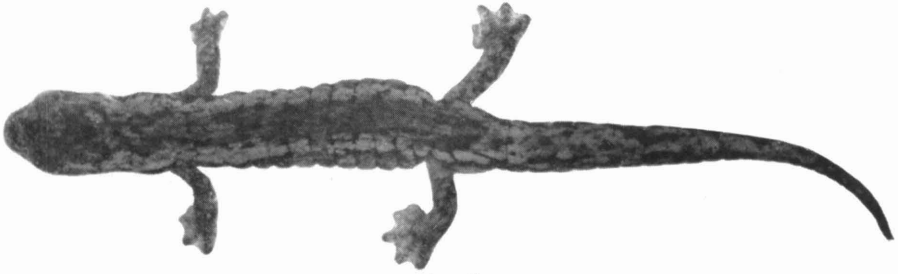


FIG. 2



FIG. 3

PLATE II

Illustration of phylogenetic change in pattern from *O. platydactylus* to *O. mulleri*.

FIG. 1.—*Oedipus platydactylus*, one of series No. 85440, slightly reduced.

FIG. 2.—*Oedipus mexicanus*, American Museum of Natural History, No. 45343, slightly enlarged.

FIG. 3. *Oedipus odonnelli*, paratype, No. 89097, slightly reduced.

FIG. 4.—*Oedipus mulleri*, No. 89127, slightly reduced.

PLATE II

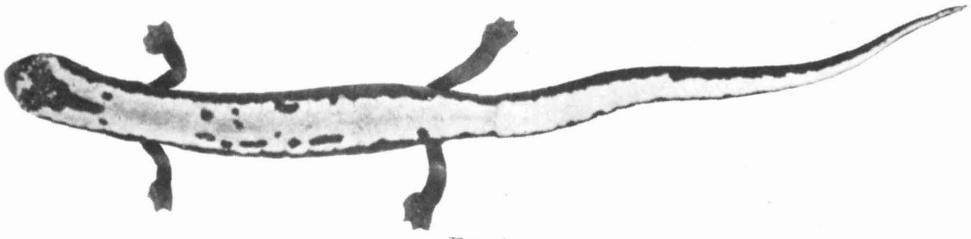


FIG. 1



FIG. 2

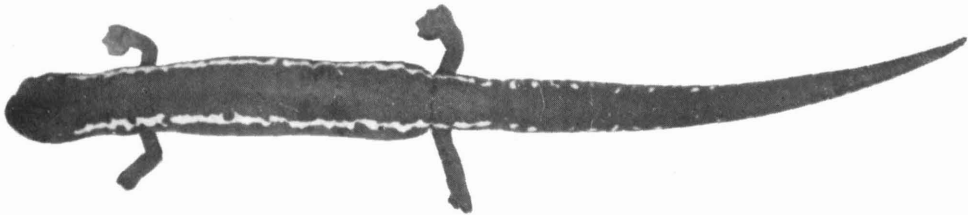


FIG. 3



FIG. 4





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