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## An Analysis of Variation in a South American Snake, Catesby's Snail- Sucker (*Dipsas catesbyi* Sentzen)

BY JAMES A. PETERS<sup>1</sup>

### INTRODUCTION

There can be little question that the collection made in Peru by the late Dr. Harvey Bassler represent one of the most significant sources of information concerning South American snakes currently available to herpetologists. The large series from restricted localities provide the first real basis for thorough statistical analysis and permit direct comparison with similar studies on North American species for the first time. Oliver (1948) used Bassler's material to good advantage in his review of the genus *Thalerophis*, and Schmidt (1952, p. 25) has found the series of *Micrurus* to be "about as extensive as the collections in all the museums of the world combined." Included in the Bassler collections is a series of 277 specimens of *Dipsas catesbyi* Sentzen, a number that doubled the total available material of that species used by myself in a revision of the subfamily Dipsadinae. I have utilized this material to gain some knowledge of the extent of variation possible within a single species of the genus *Dipsas*, which is notorious for its extremely variable species, a fact attested to by the multiplicity of synonyms of each species name. The information so gained has been extrapolated for use in the study of the variation of other species of the genus, on the assumption that the extent of variation demonstrably true in one species is theoretically true, at least in part, of other species that are closely related.

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<sup>1</sup> Brown University, Providence, Rhode Island.

One of the finest series in the Bassler material comes from the region near Iquitos, Peru. This sample includes 103 females and 105 males from a comparatively small area, and I have considered it to be representative of a single genetic population. This series has been used as the basis for comparison of variation within a single population with variation in the species as a whole and is referred to as the Iquitos population.

I have followed Oliver (1948, p. 166) in the definition and use of the terms "normally" and "usually" and have adopted them for use in both the present paper and the detailed study of the subfamily to which it belongs. He states that the terms "... are used to describe conditions that exist in 75 per cent or more of a population." In the description of *D. catesbyi* that follows, only characters that are "usual" in the above sense are included, and variations of that character are mentioned only in the general discussion of variation that follows the description.

I would like to extend my most cordial thanks to the persons who made it possible for me to see material in their care. Specimens were lent to me by the following institutions (with the abbreviations used in reference to their specimens): the American Museum of Natural History (A.M.N.H.); Academy of Natural Sciences of Philadelphia (A.N.S.P.); British Museum (Natural History) (B.M.N.H.); Carnegie Museum (C.M.); Chicago Natural History Museum (C.N.H.M.); Escuela Politécnica Nacional de Ecuador, Quito (E.P.N.); Museum of Comparative Zoölogy, Harvard College (M.C.Z.); Museu Nacional do Brasil, Rio de Janeiro (M.N.B.); Museu Paulista, São Paulo, Brazil (M.P.); Stanford University Natural History Museum (S.U.); and University of Michigan Museum of Zoology (U.M.M.Z.).

*Dipsas catesbyi* Sentzen

*Coluber catesbeji* SENTZEN, 1796, p. 66.

*Dipsas catesbyi*, BOIE, 1827, p. 560.

*Stremmatognathus catesbyi*, DUMÉRIL, BIBRON, AND DUMÉRIL, 1854, p. 522.

*Leptognathus catesbyi*, GÜNTHER, 1858, p. 180.

*Leptognathus catesbyi* [sic], PETERS, 1871, p. 402.

*Cochliophagus Catesbyi*, BERG, 1901, p. 291.

*Sibynomorphus catesbeji*, BARBOUR AND NOBLE, 1920, p. 620.

*Sibynomorphus catesbyi*, AMARAL, 1926, p. 27.

*Sibynomorphus catesbyei*, AMARAL, 1929, p. 196.

HOLOTYPE: Two cotypes, present location unknown.

RANGE: Amazonas region of South America, from Andean slopes of Bolivia, Peru, Ecuador, and Colombia to the coast of British Guiana, and through the northern half of Brazil (fig. 1).

DESCRIPTION: Rostral much broader than deep, scarcely visible from

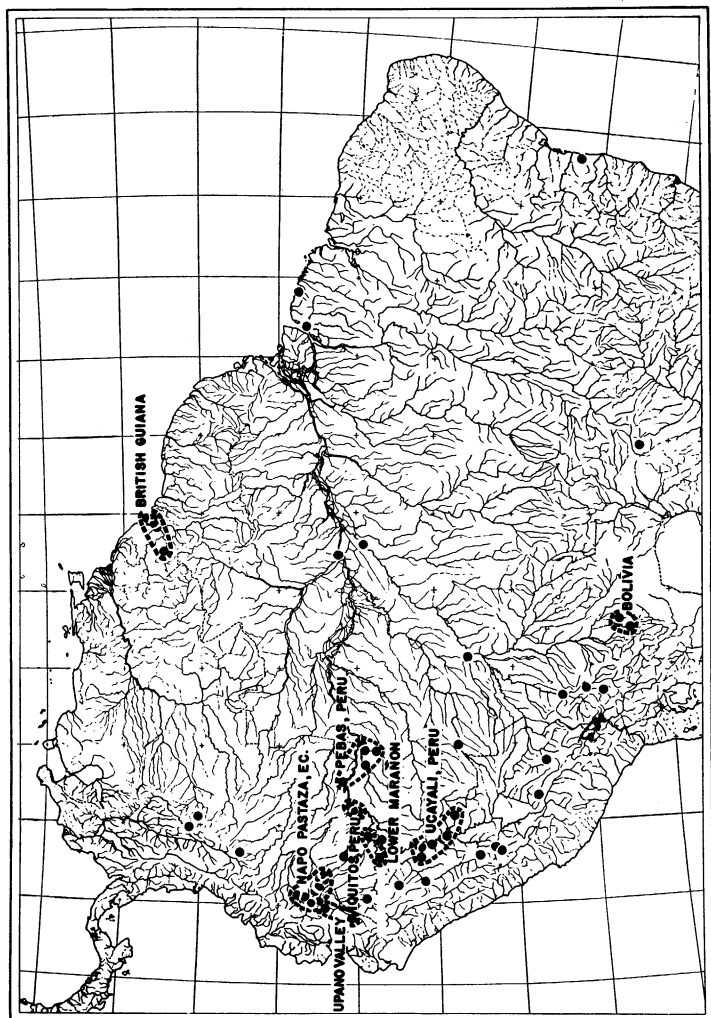


FIG. 1. Geographic distribution of *Dipsas catesbyi*. Each spot represents a locality from whence at least one specimen is known; dashed lines indicate localities included in each of named population samples.

above; internasals one-third to two-thirds of length of prefrontals, which do not enter eyes; frontal width and length approximately equal, often slightly broader than long, only slightly shorter than parietals; nasal not divided; loreal not in eye; preoculars two; postoculars one or two; suboculars none; primary temporals one; secondary temporals two; tertiary temporals two; upper labials eight or nine, fourth and fifth or fifth and sixth in eye; none enlarged. Lower labials eight to 11, none or one pair of labials in contact behind mental, four or five pairs in contact with first pair of chin shields; three or four pairs of chin shields.

Ventrals 164–202 in males, 167–189 in females; anal entire; subcaudals 86–118 in males, 77–102 in females. Dorsal scale rows 13 from level of third or fourth ventral to anus; vertebral row moderately to broadly enlarged.

Dorsal ground color light brown to reddish brown, with 14 to 40 dark brown to black blotches on body, first blotch elongate, squared, twice length of remaining blotches, which are rounded above and below; prominent white border on each blotch; blotches in some contact when opposing, even far posteriorly, but usually alternating over most of body; interspaces unicolor, lack spotting or stippling. Venter light cream, with dorsal blotches meeting or closely approximated and no spots between them anteriorly, ends of blotches widely separated posteriorly, with large, rectangular spots between neighboring blotches. Tail as in body, with seven to 20 dorsal blotches, when countable.

Dorsum of head unicolored dark brown to black, with whitish collar on occipitals and nape of neck that includes posterior labials and temporals; white stripe across snout from labial to labial, through loreals and along anterior edge of prefrontals, labials, without white spots. Dorsal markings fairly continuous or occasionally broken up across chin, nuchal collar broader ventrally, extends anteriorly on chin shields; snout stripe runs across first chin shields.

#### SPECIMENS EXAMINED

The list includes all specimens from localities not included in the several analyses of populational variation. See below for a list of specimens assigned to specific populational samples.

LOCALITY UNKNOWN: M.P. No. 1636.

SOUTH AMERICA: U.M.M.Z. No. 65856.

BOLIVIA: Beni, A.M.N.H. Nos. 2978–2984; "Bolivia," C.N.H.M. Nos. 35711, 35717; Espia, A.M.N.H. No. 21245; Huachi, A.M.N.H. Nos. 22485–22486; Manoa, U.M.M.Z. Nos. 56869, 56813; Rurrenabaque, A.M.N.H. No. 22444.

BRAZIL: Amazonas: Borba, M.N.B. Nos. 1469–1472; Manáos, A.M.N.H. No. 64905. Bahia: Itabuna, M.P. No. 1288. Mato Grosso: Rio Jaurú, M.N.B.

No. 686. Pará: Belém, M.N.B. No. 680; Bragança, M.N.B. No. 682; "Para," M.N.B. No. 681, M.C.Z. No. 5692; Tapirinha, M.C.Z. No. 2941. Territory of Acre: Alto Rio Purús, M.P. No. 2494. "Brazil," A.M.N.H. No. 3945, C.M. Nos. 2034, 22056, M.C.Z. No. 3340.

COLOMBIA: Bogotá, M.C.Z. No. 19208; Morelia, A.N.S.P. No. 25845; Rio Putomayo, C.N.H.M. No. 37442; Villavicencio, M.C.Z. No. 17648, U.M.M.Z. No. 78279.

ECUADOR: Hacienda San Ignacio, Pumasqui, E.P.N. No. 77-81; "Ecuador," M.C.Z. No. 12418; "Oriente," E.P.N. No. 711.

PERU: Cerro Puco Alto, M.C.Z. No. 45934; Chanchamayo, A.M.N.H. Nos. 52181, 52185, 52189, C.N.H.M. Nos. 40055, 40056, M.C.Z. Nos. 7455, 42442, 42443; Hacienda Pampayacu, M.C.Z. Nos. 42419, 42420; Huadquiña, M.C.Z. No. 10772; Isla Lupuna, A.M.N.H. No. 53282; Maldonado, A.M.N.H. No. 56144; Marcapata, C.N.H.M. No. 62959; Madre de Dios, C.N.H.M. No. 40054; Moyabamba, A.M.N.H. No. 53313; Rio Nanay, A.M.N.H. No. 52512; Naranjal Hacienda, M.C.Z. Nos. 45932, 45933; Pachisa, A.M.N.H. No. 52568; Perene, A.M.N.H. Nos. 23340-23342, 23353, 23363, 23382, 23397, 23401-23408, 23411-23412; "Peru," A.M.N.H. Nos. 17500, 53600, C.N.H.M. Nos. 40048-40053, A.N.S.P. Nos. 11573-11578; Pozuzo, B.M.N.H. No. 1881.5.13.89, C.N.H.M. No. 5578; Puente Asis, A.M.N.H. No. 53455; Rio Samiria, A.M.N.H. Nos. 57263, 57268; Rio Santiago, A.M.N.H. Nos. 53248, 53249; upper Ucayali River, A.M.N.H. No. 71164.

The following list includes all specimens from localities included in the populational samples. The paragraph heading corresponds to the name assigned that sample in the analyses below.

BRITISH GUIANA: Bonasica, A.M.N.H. No. 18153; Demerara River, U.M.M.Z. No. 80422; Dunoon, U.M.M.Z. Nos. 53918, 53935, 53936; Georgetown, A.M.N.H. No. 17679; Kamakusa, A.M.N.H. Nos. 25034, 25036; Kartabo, A.M.N.H. Nos. 18152, 21283; Paruima Mission, U.M.M.Z. No. 85286.

BOLIVIA: Buenavista, A.M.N.H. No. 35995, C.M. No. 2884, C.N.H.M. Nos. 35712-35716, 35718-35722, U.M.M.Z. Nos. 60646, 60800, 60801, 63180-63182, 67955, 67956, 67957 (4), 67959, 67960 (2), 67961 (6), 71368; Las Juntas, Santa Cruz de la Sierra, C.M. Nos. 20, 21, 28; Surutis, C.M. No. 2838; Rio Sirutu, U.M.M.Z. No. 63217.

IQUITOS, PERU: Iquitos, A.M.N.H. Nos. 17499, 52076, 52077, 52151, 52159, 52321, 52425, 52427, 52494, 52505, 52592, 52652, 52661, 52707, 52752, 52848, 52852, 52853, 52861, 52970, 53061, 53062, 53077, 53155, 53220, 53262, 53267, 53273, 53499, 56029, 56084, 56112, 56114, 56120; Puesto Carachama, A.M.N.H. Nos. 53188, 53194; Rio Itaya, A.M.N.H., 172 specimens; Rio Nanay, A.M.N.H. No. 52512; San Antonio, A.M.N.H. No. 52922; Santa Teresa, A.M.N.H. No. 53177.

LOWER MARAÑON, PERU: Monte Carmelo, A.M.N.H. Nos. 55551, 55552, 55559, 55567, 55569, 55571, 55577, 55580, 55584, 55586-55588, 55592, 55597-55599, 55601, 55603, 55650, 55914; Parinari, A.M.N.H. Nos. 55678, 55682.

NAPO-PASTAZA, ECUADOR: Arapina, E.P.N. No. 82; Canelos, A.M.N.H. Nos. 35875, 35876, E.P.N. Nos. 84, 731-733; Chichirota, E.P.N. No. 87; Chiguaza, E.P.N. Nos. 702, 703, 721-724; Rio Corrientes, E.P.N. Nos. 727, 728; Rio Cotopino, E.P.N. No. 83, U.M.M.Z. No. 92016; Macuma, E.P.N. No. 707;

Montalvo, E.P.N. No. 76; Rio Napo, U.M.M.Z. No. 88975; Rio Oglán, E.P.N. Nos. 725, 726; Rio Pastaza, U.M.M.Z. Nos. 88971–88974; Rio Pucayacu, E.P.N. Nos. 85, 86; Puyo, E.P.N. No. 709; Rio Sandalias, E.P.N. Nos. 734–736; Santa Rosa, A.M.N.H. No. 49175; Rio Solis, E.P.N. No. 716; Tambo Union, E.P.N. Nos. 700, 720.

PEBAS, PERU: Brazil: Benjamin Constant, M.N.B. Nos. 1291, 1292; Rio Itecoahy, M.N.B. Nos. 1468, 1473–1478; Rio Javary, M.N.B. Nos. 683–685. Colombia: Leticia, M.C.Z. Nos. 48973–48975. Peru: Pebas, C.N.H.M. Nos. 4070, 4071, M.C.Z. No. 12421, S.U. Nos. 8721, 12487, 12488.

UCAYALI RIVER, PERU: Cashiboya, A.M.N.H. Nos. 52309, 52826, 52830, 53131; Rio Cushtabatay, A.M.N.H. Nos. 52276, 53237; Orellana, A.M.N.H. Nos. 52910, 52979–52981; Pampa Hermosa, A.M.N.H. Nos. 53557, 55385, 55446, 55838, 55849, 55896, 56001, 56021; Rio Ponaza, A.M.N.H. No. 52816; Pucallpa, A.M.N.H. No. 71161, C.N.H.M. Nos. 56142, 56143; Roaboya, A.M.N.H. Nos. 52543, 52713, 54445; Rio Tamaya, A.M.N.H. Nos. 55342, 55344; Yarina Cocha, C.N.H.M. No. 56144.

UPANO VALLEY, ECUADOR: Gualaquiza, A.M.N.H. Nos. 25179–25182; Macas, E.P.N. Nos. 729, 730, A.M.N.H. Nos. 28826, 28836, 28856, 28857, 35810, 35812, 35829, 35842, 35843, 35857, 35858; Riobamba, A.M.N.H. Nos. 15211, 15216, 23282, 35902–35905, 35907–35909, 35918.

## INDIVIDUAL VARIATION

There are variations between individuals of this species in many scale characters that are the equivalent of scalation differences between some genera of colubrid snakes. These variations as well as many others occur sporadically throughout the range of the species and show no correlation with either external or internal factors, such as the environment, ontogeny, and so on. The Iquitos series gives a clear picture of individual variation in a single genetic population, and the species as a whole is compared with it.

**DORSAL HEAD SCALES:** Three individuals in the Iquitos sample show variations in the normal internasal pattern. In two, one of the pair of internasal scales has an extra suture, running lengthwise from the rostral to the prefrontal, while in the third the internasal on either side is fused with the prefrontal posterior to it, although the midline suture remains, from rostral to frontal. There are three individuals that possess internasal variations in the rest of the specimens examined. One, from Bolivia, has the lengthwise suture on its right internasal, as above, while a second, from British Guiana, has an azygous scale between the two internasals, which is not obviously split off either of them. The third specimen, from Peru, shows a partial fusion between the internasal and prefrontal on the right side only.

There are nine individuals with abnormalities in the prefrontal scales. Those with the prefrontal-internasal fusion mentioned in the last paragraph are included. Four are from the Iquitos series. Two have the pre-

frontals completely fused into a single scale, while a third has the suture between the prefrontals present anteriorly only. The fourth has the prefrontal-internasal fusion. Of the five other specimens, two, one from Ecuador and the other from Peru, have the prefrontal fused with the upper preocular on the side of the head. In addition, the one from Peru has an azygous scale between the prefrontals, separating them completely. A third, also from Peru, has the prefrontals completely fused into a single scale, and a fourth, from "Brazil," has the scales incompletely fused, with the anterior half of the suture remaining. The fifth specimen has the prefrontal-internasal fusion.

Two specimens show irregularity in the frontal shield. One of the Iquitos series has the frontal partially fused with the parietals at the midline, and a specimen from elsewhere in Peru has the frontal entirely fused with the parietals, although the suture between the parietals is complete.

Parietal irregularities, including those involving the frontal, are found in 11 specimens. Four Iquitos specimens are included, the first mentioned above, the second with partial fusion of the two parietal shields, the third with fusion between the parietal and the supraocular on the right side only, and the fourth with the upper postocular on both sides partially fused with the parietal. In addition to the specimen with a fronto-parietal fusion mentioned above, three individuals, one Peruvian and two from Bolivia, show fusion between the parietal and scales in the temporal region. Three others, all from Ecuador, have a fusion between the parietal and a postocular scale.

Many of the variations in the lateral head scales show some slight geographical correlation and are discussed under that heading. However, there are several minor variations, distributed at random throughout the range of the population. Thus the nasal scale is either partially or totally divided by a suture in 32 specimens, from all parts of the range, while it is entire in the other 407 specimens for which it was determinable. A single individual (A.M.N.H. No. 11574), from Peru, has the nasal fused with the first upper labial on both sides. A horizontal suture runs from the nostril to the posterior edge of the nasal on a single Iquitos specimen. The loreal, which is usually excluded from the orbit, is occasionally recorded otherwise, as a result of two alternative situations. On some individuals the loreal has a narrow posterior extension, which is wedged between the preoculars, with its tip entering the eye, and others have a fusion between the loreal and the lower preocular, forming a large scale which, of course, enters the orbit. Five specimens from Iquitos have the loreal in the orbit on both sides of the head, while 18 individuals from other parts of the range exhibit the same character. Eleven specimens

have the loreal in the orbit on one side only, four of which come from Iquitos. The character was recorded for 465 specimens, thus approximately 7 per cent are other than usual. One individual, from British Guiana, has the loreal horizontally sutured near the upper border, producing an extra scale between the loreal and the prefrontal. The ocular scales are sometimes fused with other head scales, and the fusions between the loreal and the lower preocular are discussed above. The upper preocular is fused with the prefrontal in one Iquitos specimen on the left side, while two specimens from the remainder, one from Peru and one Ecuadorian, have similar fusions. Two Iquitos individuals have the upper postocular fused with the supraocular, and the same is true of four specimens from the remainder, three from Peru and the fourth from Ecuador. One Iquitos specimen has a long posterior extension on the upper postocular, which separates the primary temporal from the parietal.

Most of the variation in ocular scales displayed by the species as a whole is duplicated by the Iquitos series (table 1). Both of the speci-

TABLE 1  
INDIVIDUAL VARIATION IN THE OCULAR SCALES OF *Dipsas catesbyi*

	Iquitos, Peru	Elsewhere
Preoculars		
0-0	—	2
1-1	3	13
1-2	5	8
1-3	—	1
2-2	176	217
2-3	9	17
3-3	10	8
Postoculars		
1-1	17	37
1-2	22	36
1-3	2	1
2-2	146	162
2-3	12	21
2-4	—	1
3-3	6	5
Suboculars		
0-0	191	242
0-1	13	14
1-1	5	9
1-2	—	1
2-2	—	1

mens with no preoculars on either side of the head are from the Upano Valley, Ecuador, but there are 19 others from there with the normal 2-2 preoculars. Similarly, the only specimen with two suboculars under each eye is from Bolivia, but all other individuals from there have no suboculars at all. There is no obvious correlation between any external factor and these scales.

Variations in the temporal scales are not uncommon, but 332 of the specimens examined had a single primary with two secondary temporals on both sides of the head. There were 38 individuals with two primary temporals on one side only, and 31 with double primaries on both sides, in the material examined. The secondary temporals are occasionally reduced to one, with 22 specimens having that condition on both sides, and 44 on one side only. There were four individuals with three on a single side only, and two with three secondaries on both sides. Additional analysis of the temporal scales is given in the evaluation of the populations.

The total range of variation in the number of upper labials in this species is the equivalent of that for the entire genus, i.e., from six to 11. The Iquitos series itself includes one individual with six labials on one side of the head, and there are five sides with 10 labials in the population sample. A direct comparison of the Iquitos series with the rest of the species shows that almost all the variation expressed by the entire species can be observed in a large sample from a single population (table 2). There are no specimens from Iquitos with 11 labials, and there are none with only the third labial entering the eye. With these exceptions, the series duplicates any variation (but not combination) shown in the entire species.

There is a total of 94 per cent of the individuals in the species that have either eight or nine upper labials, and these are obviously the normal numbers for the species. Only 80 per cent have either the fourth and fifth or the fifth and sixth labials in the eye, but if those with the fourth, fifth, and sixth in the eye are added to that total, 94 per cent of the individuals are included. This provides some information to aid in the localization of the change from eight to nine labials. It appears that this can occur in two ways. Either a scale is added anterior to the eye (preorbital), so that the fourth and fifth become the fifth and sixth, or three scales replace the two entering the eye (orbital), so that the addition has taken place in the orbital series. These are about equally common variations, with 114 of the first and 124 of the second, and when combined with the number of what might be called the basic pattern, i.e., eight upper labials with the fourth and fifth in the eye, a total of 87 per cent of the sides is included.

It has been noted in other tropical genera of colubrid snakes that variations in upper labial counts are usually due to fusions and divisions of

TABLE 2  
CORRELATION BETWEEN UPPER LABIALS AND LABIALS THAT ENTER  
THE ORBIT

	Iquitos, Peru	Elsewhere
Six labials		
3*	—	1
3-4	—	1
4	—	1
Seven labials		
3-4	3	12
3-5	1	2
4	1	2
4-5	—	9
Eight labials		
3-4	—	1
3-5	—	5
3-6	—	1
4	—	1
4-5	276	316
4-6	11	6
5	6	3
5-6	2	—
Nine labials		
4-5	9	19
4-6	40	63
5	2	—
5-6	54	55
5-7	—	1
6-7	—	1
Ten labials		
4-6	1	2
4-7	1	—
5	—	1
5-6	—	3
5-7	3	3
Eleven labials		
4-6	—	1
4-7	—	1
6-8	—	1

\* All figures in the left-hand column refer to the orbital labials.

labials anterior to the eye. Stuart (1941, p. 16) says, "... loss of labials in *Dryadophis* is always anterior to the orbit." Oliver (1948, p. 187) states, "... it is apparent that the difference in number of these plates involves the area anterior to the eye rather than that behind the eye." In *Dipsas catesbyi*, however, there are preorbital, postorbital, and orbital

differences in number. Variations do not occur in all three areas equally frequently. The basic pattern consists of three preorbital, two orbital, and three postorbital labials. There are 163 sides with other than three preorbital labials, and 161 with other than two orbital labials. But there are only 74 sides with other than three postorbital labials, which indicates that variations occur at about half of the frequency behind the eye as elsewhere on the lip line.

There are 30 different recorded combinations between the total number of labials and the orbital labials (table 2). These categories can be analyzed as to where the variation from the basic pattern has taken place. In eight combinations, there is variation in only one of the three areas (i.e., preorbital, postorbital, and orbital), there are 16 different categories that vary in two areas, and there are five that vary in all three parts of the labial row. When more than one area is involved, the variations are of the same kind (i.e., either all fusions or all divisions of labials) in nine categories, and eight others have fusions in one area with divisions elsewhere. Four categories result from neither fusions nor divisions but are a result of rearrangement of the eight labials in the basic pattern. Thus eight labials with only the fifth in the eye is a result of crowding the fourth out of the orbit through an expansion of the fifth, and so on.

A comparison of the basic pattern of three preorbital, two orbital, and three postorbital labials with the known variations shows that there is a greater tendency for a scale to be added through a division than for one to be lost through fusion, except perhaps postorbitally (table 3). This might indicate that eight labials are a visual expression of some unknown selective factor, and that they have been derived from slightly higher counts through one preorbital and one orbital fusion. In addition, the condition of eight labials is fairly recent in origin, and genetic mechanisms governing its appearance are not completely fixed.

TABLE 3  
COMPARISON OF NUMBER OF LABIALS OCCUPYING DIFFERENT  
AREAS OF UPPER LIP  
(The labials are oriented with regard to the eye.)

Number of Labials	Preorbital	Orbital	Postorbital
1	—	18	1
2	27	761	36
3	759	141	748
4	134	2	36
5	2	—	1

In addition to the variations in the number of upper labials, there are several anomalous situations that occur sporadically and individually. Thus five specimens have at least a single labial divided to form two scales, one above the other. Two are from Iquitos, two are from elsewhere in Peru, and the fifth is from Bolivia. In four cases there is a horizontal suture on the labial, dividing it into two approximately equal parts, while on the fifth (A.N.S.P. No. 11576) the fifth labial on the right side has a small split off its upper posterior corner. Two of the five as well as three additional individuals have a pair of labials in contact above the labial between them. Thus, on U.M.M.Z. No. 67955, the fourth and sixth labial are in contact above the fifth, which is consequently excluded from the orbit. Two of these are Peruvian (one from Iquitos), two are Bolivian, and one is Ecuadorian in origin. In addition to these variations, there are the 16 specimens, mentioned above, that show fusions between a labial and a scale in the temporal series.

There is comparatively little variation in the lower labials, beyond differences in number. No specimen is recorded as having a pair of labials in contact below the scale between them, although this is not uncommon in other species of the genus. One specimen, from Peru, has the second lower labial on the right in contact with the mental, thus preventing the first labial from touching the first labial on the left at the midline. Several individuals have the first labial on one side reaching the midline, while the first on the other side is separated from the midline by the first chin shield. This situation was not distinguished from that recorded as no contact between first labials, i.e., when neither first labial reaches the midline, and both members of the first pair of chin shields touch the mental.

The paired chin shields are either three or four in the majority of cases. Four individuals have only two pairs—two from Brazil, one from Peru, and one from Ecuador. Seven additional specimens have two on one side with three on the other. Of these, three are from Iquitos, two are from elsewhere in Peru, one is from Colombia, and one is from Ecuador. Two specimens have five pairs—one from Brazil and one from Peru. Two others have five on one side paired with four on the other—one is from Iquitos, the other is from Ecuador. Of the remainder, that is, those having three or four chin shields, there are 644 sides with three and 282 with four. Put in a slightly different way, 280 specimens have three pairs, 101 individuals have four pairs, 78 have three scales on one side with four on the other, seven have 2-3, and two have 4-5. The asymmetry results from either a fusion of two scales on one side or an extra division of a single scale, and is usually detectable. Four specimens, two from Iquitos, one Ecuadorian, and the fourth Bolivian, have unpaired median scales separating pairs of chin shields.

The body scales are, for the most part, quite uniform over the body. There is a compound reduction immediately behind the head, usually laterally, that brings the scale count to 13 at the level of the fifth or sixth ventral, and this number is then constant to the anus. The vertebral row is very broad, and the broadened scales start at the posterior border of the parietal or within a few scale rows of it. In the Iquitos series, however, there are 19 specimens that show irregularities in their dorsal scales. Some are reductions in number to 12 or 11, some increase to 14 or 15, and a few individuals have a complicated formula, including both reductions and increases.

Seven of the 19 show reductions only. Four of these have areas with only 11 scales as a result of fusion of the sixth row of scales with the vertebral row. Three of these have only a single such reduction, involving only a few scales, but the fourth (A.M.N.H. No. 54736) has the following formula :

$$(4) 13 \frac{V + 6(7)}{V + 6(8)} 11 \frac{V - 6(24)}{V - 6(16)} 13 \frac{V + 6(27, 44-45, 50-51)}{V + 6(28-29, 33-40)} 13 (182).$$

Three specimens have lateral reductions, two on one side only. One individual has the third and fourth row fused for about 30 scale rows on the anterior portion of the body, a second has the second and third rows fused for five ventrals, far posteriorly. Both return to the normal number by an addition of the third row. The third specimen, A.M.N.H. No. 54515, is unique among all the specimens seen in that the first scale row fuses with the ventral scale to reduce the count to 12, thus :

$$15 \frac{3 + 4(5)}{\text{Ventral} + 1(3)} 14 \frac{3 + 4(5)}{3 + 4(5)} 12 \frac{3 + 4(5)}{\text{Ventral} - 1(11)} 13 (185).$$

Ten individuals have an increase in the number of scale rows, to 14 or 15. The increase is lateral in two cases, both of which add an extra fourth row very shortly before the anus. All other increases are vertebral. There are two ways in which scales are added vertebally: first, by a division of the large vertebral scale into two equal scales, or second, by the addition of a seventh scale row through a lateral division of the vertebral scale. The first results in loss of a vertebral row and an even number of scales, while the second, which is usually symmetrical, results in retention of a narrowed vertebral row and an odd number of scale rows. The first was observed in six specimens (one of which also has a lateral increase). Five of these have only a single vertebral scale divided; the sixth has six such divisions. Three specimens have added rows between the vertebral and the sixth row. Two of them have vertebral divisions correlated with divided ventral scales, to accommodate the extra scale row.

The vertebral division is usually diagonal to the division of the ventral. The third specimen has a very irregular pattern, with the vertebral row split to provide a seventh and even occasionally an eighth row of scales, from the level of the sixty-fifth ventral to the anus (A.M.N.H. No. 55136). Two specimens combine both increases and reductions to make an extremely complicated, irregular formula. On A.M.N.H. No. 53869 there are at least 18 changes in scale-row number. The other specimen (A.M.N.H. No. 54752) has every kind of combination possible.

A total of 29 specimens from the remainder of the material examined show variations on the normal 13 scale rows. Nine of these show reduction only. Eight have reductions involving the vertebral row. Three of the eight have only a single such reduction, while five have a long series of reductions and increases. All the latter involve fusion of the sixth scale row with the vertebral row, which results in 11 scale rows. The specimens come from all parts of the range: one from British Guiana, two Brazil, one Peru, two Ecuador, and two Bolivia. The ninth specimen, from Ecuador, has a lateral reduction, through fusion of the third and fourth scale rows, on the anterior part of the body only.

Fifteen specimens have an increase in scale-row number. Five are from Bolivia, five Brazil, one Ecuador, and four Peru. Three individuals add a lateral scale row posteriorly and thus increase the count to 15. Thus for C.N.H.M. No. 56144, from Peru, the formula is:

$$(4) \ 13 \frac{3 - 4(152)}{4 - 5(151)} \ 15 \ (177).$$

The remaining 12 all have the vertebral row divided into two equal scales to form 14 rows, none of them showing the alternate possibility of splitting a scale off the end of the vertebral, as mentioned above in the Iquitos series. Four of these have only a single division, involving only one or two vertebrae, while the rest have a multiple series of vertebral divisions.

Five individuals (two Ecuadorian, one British Guianan, one Peruvian, and one Bolivian) have multiple fusions and additions and possess both increases to 14 or 15 and reductions to 12 or 11. On several of these the vertebral does give rise to a seventh row, although this did not occur on any of the specimens with increases only. One specimen (U.M.M.Z. No. 57957D) is unique in that it has as few as nine scale rows on parts of its body. It shows a great many fusions and reductions over the body, from the level of the eighty-ninth ventral to the anus.

For the most part, the caudodorsals in this species reduce in the normal dipsadine pattern, as shown in the diagrammatical sequence (fig. 2A). There are 32 specimens from Iquitos and 49 from the others that show,

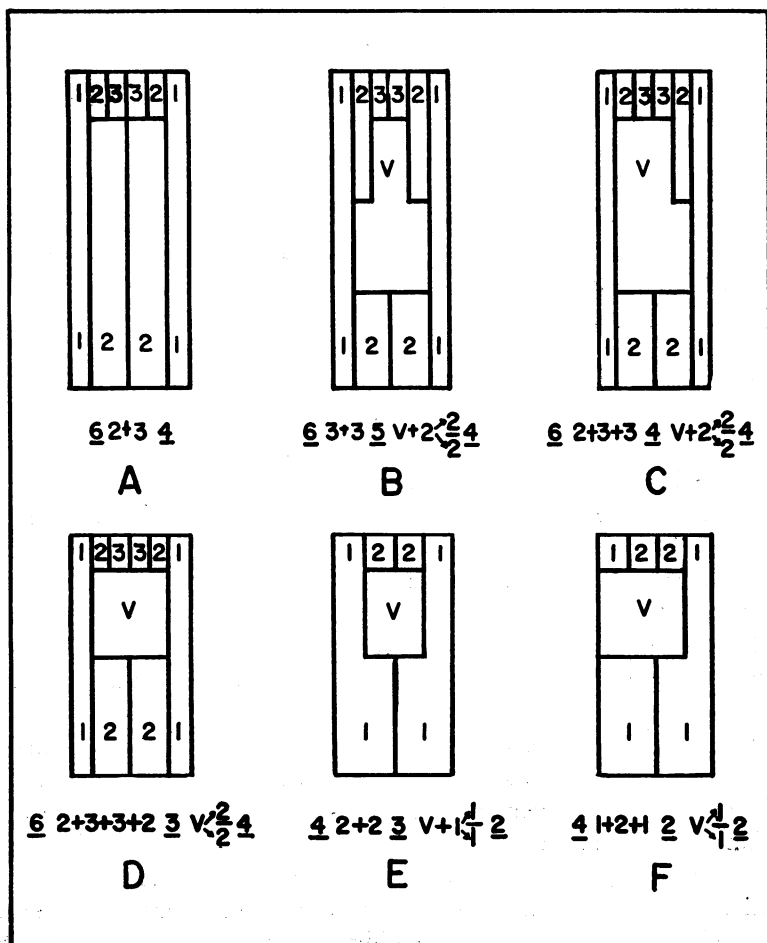


FIG. 2. Diagrammatic representation of the various formulas for caudodorsal reductions. See page 14 for fuller explanation.

however, deviations from this normal pattern. These deviations can be categorized, first as to whether they involve the decrease from six to four scale rows or that from four to two, and second as to the way in which the reduction takes place. There are 26 individuals from Iquitos with irregular reductions from six to four, and 37 from elsewhere. All involve fusions across the midline, rather than two lateral fusions, as in the normal pattern. The simplest of these (fig. 2B) is not the most common, for only eight from Iquitos and 17 from elsewhere show that formula. If a third lateral row is included in the first fusion (fig. 2C), the reduc-

tion is to four rather than five rows. In both of these formulas, the second fusion and the division of the vertebral row into lateral rows are often simultaneous, that is, they take place at the same point, so that there appears to be a narrowing of the vertebral row and an enlargement of one of the lateral rows. There are 16 from Iquitos and 20 from elsewhere with this type of reduction. The next step is the expected one, that is, inclusion of two lateral rows in the first fusion (fig. 2D), followed by a vertebral division. Only two Iquitos specimens and one from elsewhere show this type of reduction.

A total of seven individuals (two from Iquitos and five from elsewhere) show deviations only in the reduction from four rows to two. There are two ways in which this can take place. The first is similar to the first variation mentioned above and involves a cross-vertebral fusion (fig. 2E). Only one specimen shows this without other complications as well (see below). The second variation includes a fusion of all lateral scales on one side plus one scale from the other side, with a more posterior fusion with the second on the other side (fig. 2F). There are no specimens from Iquitos and four from elsewhere with this form of reduction only.

Eleven specimens show various combinations of the 6-4 and 4-2 reductions. There is some correlation between the type of reduction, that is, the same kind will repeat at both places. This is true of seven specimens. All the Iquitos specimens included, a total of four, have a combination of the third and sixth types (fig. 2C, F), which are the same in nature, while only one of the remainder does this. Two of those from elsewhere combine the second and fifth types, which are also the same in nature. The other four specimens show modified combinations. Three have combinations of the second and sixth types, while one specimen has the third combined with the fifth type. One additional specimen is anomalous, but its reduction was not annotated.

There are four individuals that show occasional deviations from the normal pattern in possessing cross-vertebral fusions that continue for only a short distance and then return to the original number. This happens most often on areas where the scale rows are four, but was also observed where there are only two rows. The result in the latter case is, of course, a single dorsal scale extending from one subcaudal to its pair.

Variations in the number of ventral scales are discussed elsewhere, for there is correlation between both sex and geographical origin in that character. The sporadic occurrence of divided ventral scales (fig. 3) appears to be completely individual, however, and such scales will be found on a few specimens of any sufficiently large series. When the

series from Iquitos, with a total of 208 specimens, is compared with the rest of the specimens examined, a total of 289, there is a close agreement in results. There are 30 specimens from Iquitos with divided ventrals, and the total for the rest is 37. Divisions of type one were found in 20 Iquitos individuals and 22 others. Type-two divisions occur in four

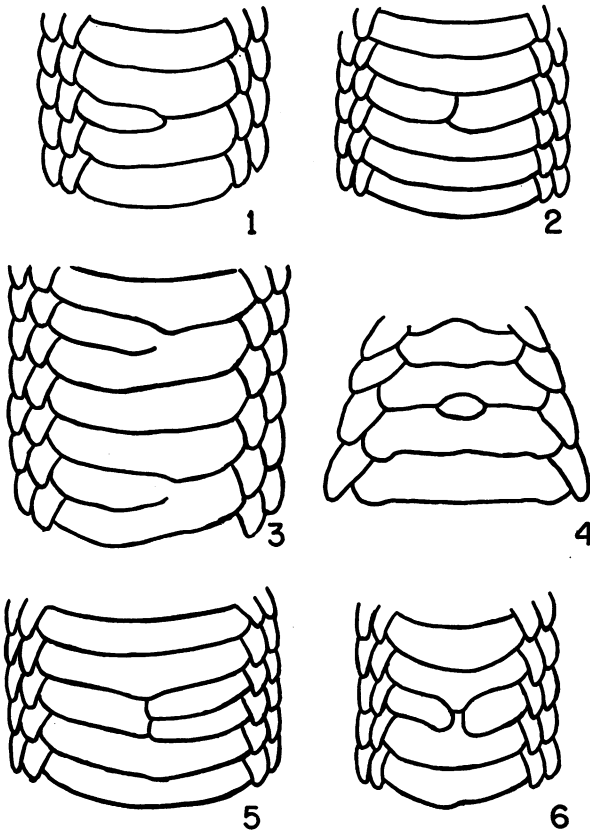


FIG. 3. The six different types of division of ventral scales known to occur in dipsadine snakes. All but the fifth have been observed in *Dipsas catesbyi*.

from Iquitos and five of the others; type-three, in five and six; type-four, in six and three; type-five, in none from either population; and type-six, in three and one. Five specimens in each group show combinations of two or more types of division. There are four additional specimens in the remainder for which the type of division was not recorded.

The majority of specimens have only a single divided ventral of each type, although two types might be represented on the same individual.

Thus there are 25 such cases from Iquitos and 35 from the remainder. Quite often the division is found in the last ventral anterior to the anal plate. This is true for 23 individuals from Iquitos and for 28 others. Occasional individuals have two or more divisions of a single type. Of the Iquitos series, three have two type-one divisions, one has four type-two divisions, and one has three type-four divisions. A truly exceptional individual (A.M.N.H. No. 53930) has 22 divisions, of which 16 are type one, three are type six, two are type three, and one is type four. This is the maximum observed in this species. In the rest of the specimens, one Peruvian individual has two type-one divisions, a second Peruvian specimen has five type-two divisions, and one from Ecuador has three type-three divisions.

There is little variation in the subcaudal scales, except in total number of pairs. A few specimens, however, show fusion between pairs, so that there is a single subcaudal scale, as is typical of a few other snake genera. Five individuals from Iquitos have fused subcaudals, and only one of these is a single pair. Three others have two to four pairs fused, and the fifth has 13 fused pairs. There are six specimens from elsewhere with fused subcaudals. Three of these have only a single pair fused. Two of them are from Bolivia; the third is from British Guiana. Another Bolivian specimen has four fused subcaudal pairs, a Peruvian specimen has five, and an Ecuadorian individual has eight.

### POPULATIONAL VARIATION

In order to analyze the variation between populations it was necessary to break the data down to a point where in each case a maximal number of specimens from a minimal area (fig. 1) was available. The Bassler collections from Peru provided the most complete series for analysis and have formed the basis for comparison throughout the study of the species *catesbyi*. It was possible to analyze four groups from Peru after combination of Bassler material with occasional specimens from other collections. The first of these, referred to elsewhere as the "Iquitos series," includes specimens from the Rio Itaya, Iquitos, San Antonio, Santa Thereza, and Puesto Carachama. A total of 208 specimens were available from this very restricted area. This is almost equivalent to the total material from elsewhere, which includes only 289 specimens. A second Peruvian series combines the material from the following localities for a total of 28 specimens: Cashiboya, Rio Cushtabatay, Orellana, Pampa Hermosa, Rio Ponaza, Pucallpa, Roaboya, Rio Tamaya, and Yarina Cocha. This series is referred to as the "Ucayali River series." A third Peruvian population, referred to as the "Lower Marañon River series,"

includes 22 specimens from three localities: Monte Carmelo, Parinari, and Rio Samiria. The fourth series of 21 specimens, called the "Pebas series," is from Pebas, Peru; Leticia, Colombia; and three Brazilian localities: Benjamin Constant, Rio Javary, and Rio Itecoahy. There are two populations from Ecuador, the first of which includes 35 specimens, all from Lower Amazonian slope localities, in Napo-Pastaza Province, while the second includes 28 specimens, all from localities in the Upano Valley, in Santiago-Zamora Province, an area drained by the Rio Marañon. The latter population includes material reportedly from Rio-bamba—a locality I believe to be erroneous for these specimens. A northern population includes 11 specimens, all that were available from British Guiana, while a southern population, from Bolivia, includes 39 specimens from Buenavista, Las Juntas, and Rio Surutu. All the remaining specimens come from widely scattered localities, and in no case are there sufficient specimens from a restricted area to permit statistical analysis. Comparison of the populations here listed is quite informative, however, and provides a certain basis for extrapolation of information to isolated individuals.

The maps in figures 4–11 are designed to show populational differences



FIG. 4. Percentage of individuals in populational samples with other than a single primary temporal. See page 21.

for various characters of scutellation. Two populations mentioned above have been omitted from these maps because of inadequate space and their basic similarities to the others shown. These are the Upano River series from Ecuador, and the Lower Marañon series from Peru. For the rest, the center of each circle represents the approximate center of this populational sample. In all circles, the black area represents the percentage of individuals possessing the character in question; thus 90 degrees in the circle represents 25 per cent of the total sample. The sexes have been combined in all cases.



FIG. 5. Percentage of individuals in populational samples with fewer than two secondary temporals. See page 21 *et seq.*

A glance at these maps is sufficient to indicate that one of the chief difficulties in the analysis is the peripheral nature of the samples. If these maps are compared with the range map (fig. 1), it is obvious that the Amazonian lowlands are of critical significance in an understanding of just what is taking place within this species. It is unfortunate that collections from this vast area are so scanty. Vanzolini, in his study of *Amphisbaena fuliginosa* Linnaeus (1951), found that he could hypothesize a central Brazilian origin for the species, with a dispersal pattern resembling the spokes of a wheel or a bomb-burst. This was particularly

noticeable in his map of the geographic differentiation of the number of body annuli (Vanzolini, 1951, p. 23). The highest counts are found in the center of the range, and there is a decrease in number of annuli radially, with the lowest values found on the periphery of the range. Several of my maps hint at such a variational pattern, but lack of material hinders validly drawing any such conclusion. Again, although sufficient material is available to provide an indication of the existence of clinal trends within *Dipsas catesbyi*, it is not sufficient to make them clearly demonstrable.



FIG. 6. Percentage of individuals in populational samples with fewer than eight upper labials. See elsewhere on this page.

Five of the eight maps (figs. 4, 7, 8, 9, and 10) show maximum differences between the Bolivian and the British Guianan series, with the Peruvian and Ecuadorian material possessing intermediate values. This might well be interpreted as an indication of a north-south trend in variation, or a cline. It should be noted, however, that, while the trend is supposedly present in the increase of the number of primary temporals (fig. 4), it is not reflected by the picture of the situation for the secondary temporals (fig. 5). Also, there appears to be a gradual increase in the number of specimens with more than eight upper labials (fig. 7), but this trend is not seen on the other map (fig. 6) of variation in these scales. On

the contrary, the Peruvian populations lack almost totally any individuals with fewer than eight upper labials, while the more outlying areas all have approximately the same percentages of such specimens. Both of the maps of variation in lower labial number (figs. 9 and 10) exhibit a rather gradual change from north to south.

In two cases the Peruvian and Ecuadorian material show maximal values, while the Bolivian and British Guianan series are approximately equal. This is true of the percentage of specimens with reduced numbers



FIG. 7. Percentage of individuals in populational samples with more than eight upper labials. See page 21 *et seq.*

of secondary temporals (fig. 5) and of those with the mental in contact with the first chin shields (fig. 11). The largest value for the latter is found in the Iquitos series, with 80 individuals out of 208 showing the character. This is almost 40 per cent.

It should be recognized that the map of those with fewer than 10 lower labials (fig. 9) and that of those with fewer than five lower labials in contact with the first pair of chin shields (fig. 8) are practically two ways of expressing the same variation. They would be identical if all the variations in lower labial count took place within the first five labials. That this

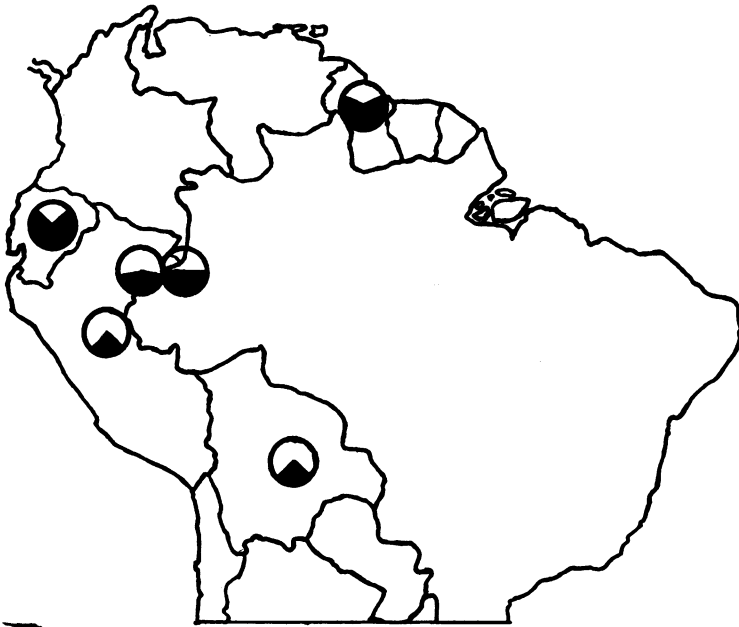


FIG. 8. Percentage of individuals in populational samples with fewer than five lower labials in contact with first pair of chin shields. See page 21 *et seq.*

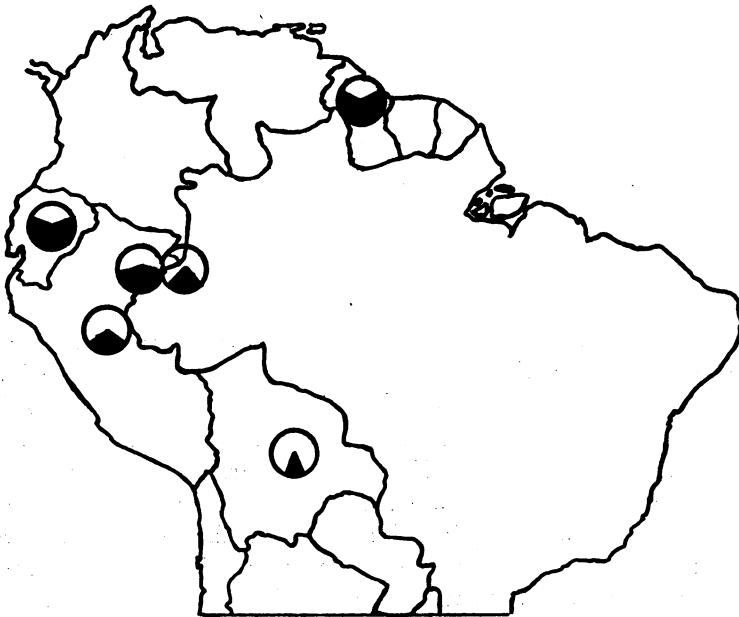


FIG. 9. Percentage of individuals in populational samples with fewer than 10 lower labials. See page 21 *et seq.*

is not true can be seen by comparison of the spots for the Pebas series, for example. These two maps do indicate, however, that both the Ecuadorian and the British Guianan series have a tendency towards a reduction in the number of lower labials.

Five of the maps (figs. 5, 7, 8, 9, and 11) show considerable differences among the three populations from Peru, while the other three show quite uniform results. In three (figs. 7, 8, and 9) of the five cases, the



FIG. 10. Percentage of individuals in populational samples with more than 10 lower labials. See page 21 *et seq.*

Ucayali River series is more similar to the Bolivian series than to either of the other two Peruvian populations. The Iquitos and Pebas series are quite similar, with the Ucayali River series strongly contrasted to them, in the case of those with fewer than five labials on the first chin shields (fig. 8). The Iquitos and the Ucayali River series are similar and contrasted to the Pebas group when the number of individuals with the mental in contact with the first chin shields is checked (fig. 11). And, finally, the Pebas and Ucayali series are more alike, with the Iquitos population strongly deviant from them, in the occurrence of individuals with fewer than 10 lower labials (fig. 9).

All these maps seem to support the contention of Wilson and Brown



FIG. 11. Percentage of individuals in populational samples with mental in contact with first chin shields. See page 22 *et seq.*

(1953, p. 104) that "geographical variation of independent characters tends to be discordant to some degree" and that "the greater the number of characters, the greater will be the total discordance." The characters on these maps are of the type that is likely to be ignored in the process of establishing subspecies within a species. I cannot avoid the conclusion, however, that these data are just as important in the evaluation of the variation within the species as are others that show statistically significant deviations from one another.

The variations in ventral counts show some populational correlation (fig. 12). The mean value for the Upano Valley material is significantly lower than that of any of the near-by populations and is closest to the British Guianan series, which was too small to permit calculation of the standard error of the mean. These variations are insufficient to provide a basis for subspecific differentiation of populations, even though the differences between the means are significant. Thus, for the females at least, the single sample from Iquitos shows a range of variation that includes all other samples within its limits, with the single exception of the Napo-Pastaza series. The latter has an upper limit of 189 ventrals, while the limit for Iquitos is 188. There is somewhat greater contrast within the

males, in that a single population does not include all the rest within its limits of variation. The highest ventral count, 202, was observed on M.P. No. 1288, from Baía State, Brazil.

A comparison of the two Ecuadorian populations alone, without regard to the remaining material, shows that in both sexes the differences between the populations is a considerable one. But while these two populations can be easily distinguished from each other, the intermediacy of the Peruvian material makes it impossible to separate them from or to combine them with other populations in such a way as to establish sub-specific lines.

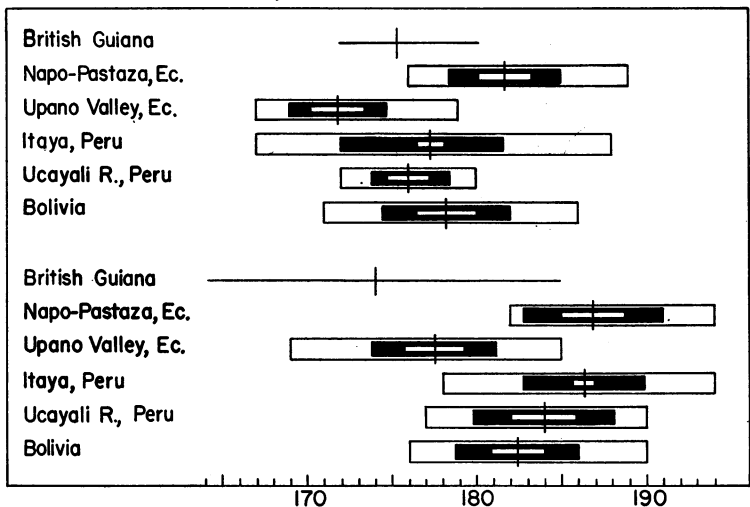


FIG. 12. Variation between populations and sexes in ventral scale counts. The vertical bar indicates the mean; the small white rectangle, four times the standard error of the mean; the black rectangle, two standard deviations; and the large white rectangle, the observed variation. Females are above, males are below.

Comparison of the variations in subcaudal counts (fig. 13) shows a picture similar to that for ventrals. One contrast between the two is that the Bolivian and British Guianan populations show minimal and approximately equal values for subcaudals, but are quite distinct from each other when the statistics for ventral scales are compared. Similar contrasts are noted above where the head scalation in various populations is compared.

The two population samples from Ecuador again show a significant difference between their means. The difference is not so great as that between the means for the ventrals in the same samples, and the overlap

between their extremes is considerable. The material from near-by Peru is again quite intermediate between them.

The only obvious correlation of subcaudal count with geographical locality appears to be that of relationship to the supposed center of dispersal for the species, i.e., central Amazonia. Those populations lying within the limits of the Amazonian lowlands, including the Peruvian material from Iquitos, and the Napo-Pastaza series have the highest mean values, as well as the maximal values. As the distance between the

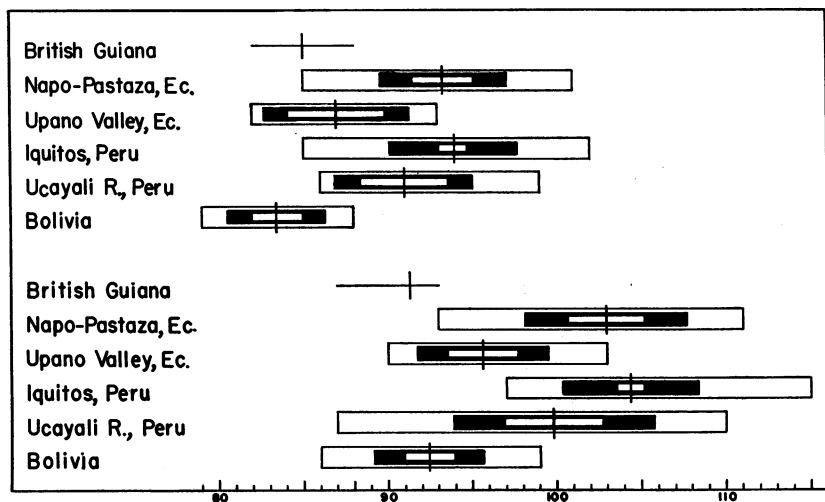


FIG. 13. Variation between populations and sexes in subcaudal scale counts. The vertical bar indicates the mean; the small white rectangle, four times the standard error of the mean; the black rectangle, two standard deviations; and the large white rectangle, the observed variation. Females are above, males are below.

point of collection of a sample and the Amazonian lowlands becomes greater, the values for subcaudal counts of the sample become lower. The Upano material and the series from the Ucayali drainage are from slightly higher localities within the Andean foothills, near the lowlands. The British Guianan material, which shows very low subcaudal counts, does not even come from an area of Amazonian drainage and is on the periphery of the range. Again, it is unfortunate that no material from mid-Ama-zonia is available. The single specimen from Manáos is a male, with a subcaudal count of 98—a value that is included within the range of every sample but one.

Because there is no apparent sexual difference in number of body blotches (see below), the sexes have been combined in the graphic analy-

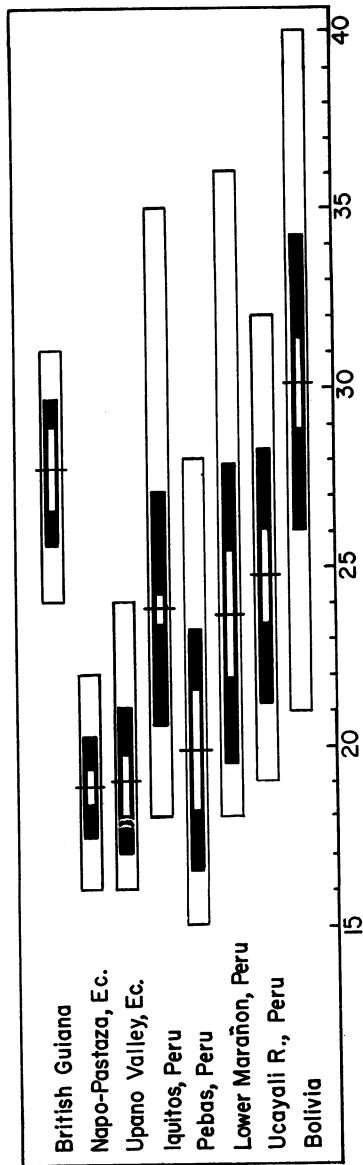


FIG. 14. Variation between populations in number of body blotches. The sexes have been combined, as there is no significant difference between them in this character. The vertical bar indicates the mean; the small white rectangle, four times the standard error of the mean; the black rectangle, two standard deviations; and the large white rectangle, the observed variation.

sis of this character (fig. 14). This makes available samples from additional localities large enough for statistical analysis, and all eight samples are included.

The populations from Bolivia and British Guiana show the highest mean values for this character. There is no significant difference between the means for the two populations, but both of the means are significantly different from those of all other populations. In addition, the Bolivian population includes the maximum value for the entire species, i.e., 40 blotches. The upper limit for British Guianan specimens is surpassed by three of the four Peruvian populations.

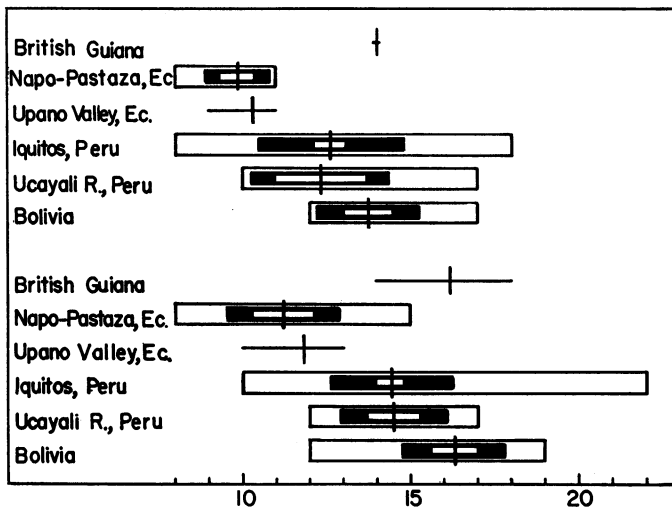


FIG. 15. Variation between populations and sexes in number of tail blotches. The vertical bar indicates the mean; the small white rectangle, four times the standard error of the mean; the black rectangle, two standard deviations; and the large white rectangle, the observed variation. Females are above, males are below.

The two Ecuadorian samples are very similar in this character, and there is no significant difference between their means. Neither of them is significantly different from the sample from Pebas, Peru, while all three of them are significantly lower than the other three Peruvian samples. Again, there are no significant differences between any of the latter. Pebas, however, is the easternmost sample from Peru and includes material from neighboring Brazil and Colombia. Both the Iquitos series and the material from the lower Marañon are from areas between that represented by the Pebas material and the two series from Ecuador and are within the same drainage systems. The Ucayali River series is from

farther south, in a different drainage. These populational differences, therefore, show no geographical correlations.

In contrast to what has been observed for the body blotches, the two sexes are definitely different in the number of tail blotches and have been separated for statistical analysis (fig. 15). As was observed in the case of the body blotches, the British Guianan and Bolivian populations are maximal in mean values. The greatest number of tail blotches occurs in neither of them, however, but is found in the Iquitos series, perhaps a reflection of its size. Sufficient material would probably demonstrate that there is little difference between these two populations and the samples from Peru. The Bolivian series, for example, is significantly different from Peruvian material in the case of the males, but this is not true for the females. There is certainly nothing distinctive between these populations when the minimum-maximum limits are considered.

On the other hand, the two Ecuadorian populations are quite distinct from the others. In only two cases is the upper limit of the range of values for an Ecuadorian sample greater than the mean value for any other population, and in those two cases it is only slightly larger. But, although the Ecuadorian samples are alike in the number of tail blotches, they are qualitatively different. The Upano Valley sample is small, and statistics other than the mean could not be calculated, as the result of an additional factor. In this series the interblotch area is very dark, as a result of invasion of the area by blotch color, and in many specimens it is quite impossible to count the blotches. This qualitative character is not marked in the Napo-Pastaza series and serves as a distinction between them.

Variations in the color pattern of dipsadine snakes are comparatively minor and are certainly not of the magnitude of variations in lepidosis. This may well be a reflection of greater selective pressure against color-pattern differences.

There are several populational characteristics in color and color pattern that are, however, of interest here. The blotch usually has a narrow white or light cream border, and when the blotches alternate bilaterally this border extends completely around each of them. This border is often partially lost, however, being present only ventrolaterally, and in the British Guianan series it is completely absent on all specimens. It is absent at least posteriorly on 65 per cent of the Upano Valley, Ecuador, series, and about 35 per cent of the Napo-Pastaza series lacks it, while another 30 per cent have it present but poorly marked. In the Bolivian series, on the other hand, it is present and prominent, and all individuals in the Peruvian populations have it, with the exception of two juveniles in the Ucayali River series, one juvenile in the Lower Marañon series, and 12

specimens, juveniles for the most part, from the Iquitos series. While the absence of the white border is more common in juveniles, it is not unique among them, for many very small specimens have clearly defined borders, nor is it restricted to them, for adults occasionally lack the borders. Another variable blotch character is exhibited by the blotches on the posterior part of the body. These blotches usually alternate bilaterally but occasionally are opposed. When they are opposed, they may fuse with each other across the vertebral line, or they may leave a small gap ventrally, with the white border complete around the top of the blotch. Again, the British Guianan population is most distinct, in that the blotches are fused if opposed in all but one specimen. In all the other population samples the majority show unfused blotches when opposed. The Ucayali River series and the material from Bolivia show the widest separation of dorsal blotches. Even when opposed, they extend only onto the outermost edges of the vertebral scales, and even the white borders are not in contact. The white borders are usually fused when opposed in all other Peruvian populations, as well as the Ecuadorian material.

Specimens from British Guiana and Bolivia show practically no fusion of the anteriormost dorsal blotches across the belly. All the other populations have different proportions of individuals with fusion of blotches ventrally and also have different numbers of blotches fused. There are three or more of the anterior blotches fused ventrally in 82 per cent of the Upano Valley series, 70 per cent of the Napo-Pastaza population, 42 per cent of the Iquitos material, 18 per cent of those from Lower Marañon, and only 7 per cent of those from the Ucayali River.

The ventral surface is usually rather heavily stippled with brown, and occasionally the stippling is heavy enough to form a mid-ventral streak. In the darkly colored population from Upano Valley, Ecuador, the stippling is extremely heavy, and the entire ventral surface is dark brown to black. The majority of specimens from most populations have at least a light stippling, but the British Guianan material has none at all or a light scattering only. The Lower Marañon series includes 17 specimens with very light stippling, but five others from that population have heavy stippling. Eleven individuals out of the large Iquitos series lack all ventral stippling; the rest have it.

Large, squarish spots are usually present ventrally between the ends of neighboring dorsal blotches. Single individuals lack them in the Ucayali River, Peru, and the British Guianan series. The spots are quite small when present in the British Guianan material. They are missing in two individuals from the Napo-Pastaza, Ecuador, series. The spots are quite elongated in some Peruvian and Bolivian specimens, and are often closely

approximated, particularly in those individuals that have somewhat smaller dorsal blotches. The over-all appearance in these specimens is that of a broken stripe rather than of discrete spots. The series from Iquitos, Peru, has 25 per cent of its individuals with this dashed striping. Occasionally several such blotches are fused, and a stripe is formed, as in A.M.N.H. No. 55678, from the Lower Marañon series, or in U.M.M.Z. Nos. 63180 and 67961E and C.N.H.M. No. 35720, all Bolivian.

With regard to the head coloration, there is variation in the nuchal stripe, the white line across the snout, and the black bar across the chin. Again the population from the Upano Valley, Ecuador, is outstanding because of the heavy melanin deposition, for almost 80 per cent lack the white line across the snout entirely, and an added 18 per cent have only a line of white spots across the snout. This population has the nuchal collar broken, usually vertebally, in 50 per cent of the individuals, and the black bar is complete across the chin in 88 per cent. No other population has this much pigment deposition on the head and neck. The Napo-Pastaza population is intermediate in all three characters between the Upano series and the rest of the species. Thus it has 62 per cent of the individuals with an incomplete snout stripe, while no other population has more than 10 per cent of its individuals with an incomplete stripe. It has 14 per cent with an incomplete nuchal collar, while only one specimen has a broken collar in all the remaining samples. It has 56 per cent of its individuals with a complete black bar across the chin, while the Iquitos series has 42 per cent with a complete bar, the Lower Marañon series has 40 per cent, and the Ucayali series has 14 per cent. It is virtually never complete in either the British Guianan or Bolivian series, but is only a scattering of black spots, usually centered in individual scales.

### ONTOGENETIC VARIATION

Any attempt at determination of the effects of ontogeny or growth on the variations exhibited by a species must be based on an assignment of individuals to age groups, which are then compared. If the entire Itaya series is plotted on a graph to show body length against number of individuals, a series of peaks and valleys can be noted (fig. 16). The actual value of this graph in the evaluation of age groups is somewhat doubtful. Certainly the work that has been done on North American snakes has indicated that it is difficult to distinguish between slower growing individuals of one age group and the more rapidly growing members of the year following it. Thus, when Fitch worked with *Pituophis catenifer*, he found that "comparatively few half-grown snakes were taken, and they could not be sorted into age groups" (1949, p. 553). He had a recorded

total of 256 snakes. Klauber (1937), working with 858 *Crotalus viridis*, plotted a histogram similar to the one given here, but found that when the increment was less than 50 mm. fluctuations occurred that tended to obscure the distribution. My increments are 10 mm., but, at the same time, maximum size for *D. catesbyi* is 580 mm., while *C. viridis* reaches 1050 mm. Klauber (1937, p. 21) does feel that a pronounced dip in the distribution pattern would permit a tentative segregation by assuming that two age groups were following a normal distribution, with overlap of the ends of their respective curves. The division into years shown in my figure 16 is based on this likelihood. It would appear from these data that there is an annual increment in length of body of approximately 50 mm. during the first four years of life. After this time sufficient variation between individuals of the progeny of a single year has accumulated to obscure the variation between the progeny of successive years.

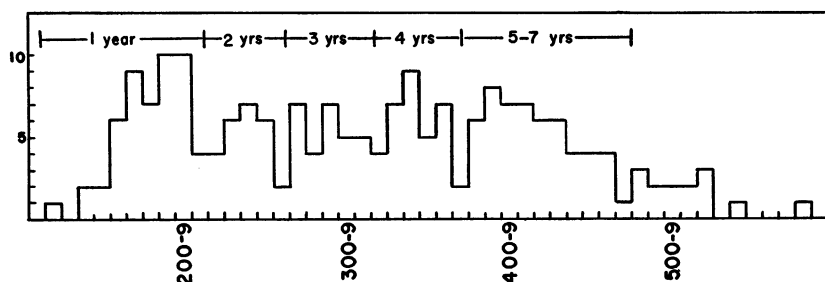


FIG. 16. Age groups within the Iquitos series. The ordinate represents the number of individuals within each of the 10-mm. size groups, which are plotted on the abscissa. The sexes are not separated.

The likelihood that differences between the sexes might be obscuring the interpretation of the graph was considered, and each sex was plotted separately for comparison. While this reduced the number of individuals to a point at which peaks and valleys were not so obvious, the groupings could still be distinguished. In no case was there more than a 10-mm. difference between modal classes for comparable individual peaks from one sex to the other. For example, the modal class in the first year group for males was the 200-209 series, while for the females it was the 190-199 series. There is a slight indication on the graph of the male series that there might be only three year groups up to 379 mm., rather than four, as shown in the figure. Further verification of the conclusion that there is little difference between the sexes as concerns growth rates was derived from plotting a Galton curve of the lengths of the entire series, in the method employed by Bergmann (1950, p. 8) in his study of *Natrix vit-*

*tata*. This graphic method is quite unsatisfactory in that it is highly dependent upon sampling methods and must rest upon the assumption that all age groups have been equally sampled (van der Vaart, 1953, p. 201). It is still indicative that there is little or no difference between the sexes of *D. catesbyi*, however, for it was found that the curves resulting from independent plots of the sexes were practically identical in both slope and position.

There is a suggestion in these data that these tropical snakes differ in a marked degree from snakes of the temperate regions with regard to growth. Carpenter (1952, p. 239) indicates that female snakes of the genus *Thamnophis* in Michigan maintain a more rapid growth rate throughout their life. On the other hand, Fitch and Glading (1947, p.

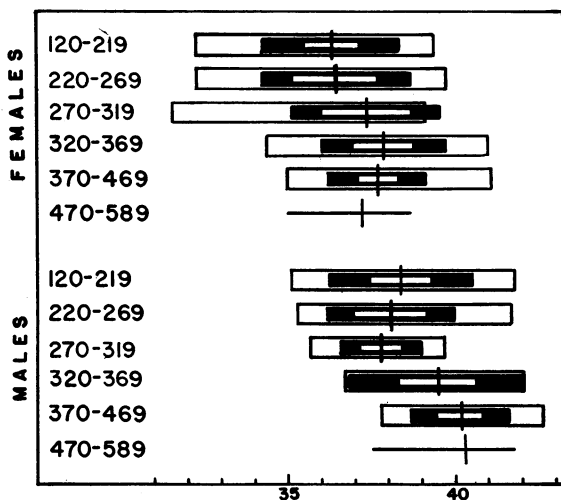


FIG. 17. Comparison of the rate of growth of the body and the tail during ontogeny. The abscissa represents the ratio of tail length/body length. The vertical bar indicates the mean; the small white rectangle, four times the standard error of the mean; the black rectangle, two standard deviations; and the large white rectangle, the observed variation.

113) found that the "... records for repeat females suggest that they grow somewhat more slowly than males." In *D. catesbyi* it appears that the rate of growth may be very similar if not identical for both sexes. Because there is no evidence concerning year-round activity in tropical snakes, and I know of no attempts to mark and recapture such species, further speculation must await comparative studies on the natural populations of tropical species.

If the data are separated into age groups corresponding to the peaks and valleys of the body length graph (fig. 16), and the ratio of tail length

to body length is calculated for each group, there appears to be a slight indication that the tail grows more rapidly than the body (fig. 17). The gradual shift to the right of the mean and the range for progressively older age groups is obviously without strong statistical significance, for there is overlap between the doubled standard errors in all the groups of the female sample and all but one group within the male sample. Klauber (1943, p. 30) found that a differential in growth rate between body and tail existed in approximately half of the 40 species examined, from all parts of the world. A majority of his samples had relatively longer tails as they aged. It is entirely possible, of course, that a longer tail possesses greater selective value as the body becomes longer and heavier, for these are arboreal snakes, dependent on the tail for survival. There might thus be set up a selective advantage in possessing a genetically controlled ontogenetic increase in tail length.

Dunn (1942) suggested that there might be demonstrable survival value in variations within a single population of snakes and demonstrated that juveniles appeared to have a wider range of variation than adults for several characters. Inger (1943) supplemented this data with information on ventrals and caudals of *Thamnophis radix* and suggested that animals with low counts of either ventrals or caudals were selected against owing to the decrease in flexibility resulting from fewer vertebral units. Both Dunn and Inger compared juveniles with all adults. Inger used juveniles of less than 200 mm. and adults of not less than 400 mm. for his comparison. I have taken advantage of the separation into age groups within the Iquitos population to learn if there is any such differential survival in this tropical species. The results (table 4) may be somewhat

TABLE 4  
COMPARISON OF ONTOGENETIC CHANGE IN THE MAXIMUM LIMITS OF VARIATION  
IN NUMBER OF VENTRALS  
(The parenthetical figures refer to the number of individuals  
included in each class.)

Size Group	Female Ventrals	Number of Included Ventrals	Male Ventrals	Number of Included Ventrals
1	171-183 (22)	13	180-196 (25)	17
2	171-184 (12)	14	183-190 (13)	8
3	171-188 (11)	18	182-193 (16)	12
4	171-182 (17)	12	178-194 (15)	17
5	169-187 (29)	18	181-192 (23)	12
6	171-187 (5)	17	182-193 (10)	12

obscured by the smaller numbers of individuals used as compared with Inger's sample, but it is enlightening to note that the smallest series among the females, with five specimens, is also the oldest size group, and the range for these individuals is greater than that for 22 individuals from the size group representing the first year animals. There is certainly little in these data to indicate that there is a decrease in variability with age in this species.

### VARIATION BETWEEN THE SEXES

There is an apparent sexual dimorphism to be observed in the material examined. It can be seen in the figures used above in the study of population variation, if plotted values for each population are compared for the two sexes. There is a statistically significant difference between the means for the ventral scales in the two sexes within every population (fig. 12), except for the British Guianan series, in which the number of available specimens was too small to permit calculation of any statistic other than the mean. The difference is even more pronounced when the sexes within each population are compared as to subcaudal counts (fig. 13). In no case is there overlap of the one standard deviation on either side of the mean. It appears, therefore, that the sexual dimorphism is more strongly reflected in the subcaudal counts than in ventral counts.

This difference between the body and the tail is again reflected when the blotch counts are compared. In the case of the Iquitos series, if the body blotches of the total population are charted as a unit, males and females combined, a fairly uniform normal curve is the result (fig. 18). Although the data were calculated separately for each population, it was found that there was no significant difference between the means for the body blotch counts of each sex within any single population. These counts were therefore combined in the graph of this character (fig. 14). On the other hand, there is a significant difference between the means of the tail blotch counts for the sexes in three of the four populations in which the sample was large enough to permit calculation of the standard error (fig. 15). The Upano Valley population is quite distinct from the rest of the species through the almost complete obliteration of the blotches on the tail. Because they cannot be counted, the series is too small to be tabulated.

A third verification of the sexual dimorphism in tail characters is seen in the tail length/body length ratio (fig. 17). Although this is plotted to show comparisons of age groups, the two sexes within a single age group can be compared as before, and it will be seen that two and possibly a third (the 470-589 group) display a significant difference between the means for the two sexes. While there is always some question as to which

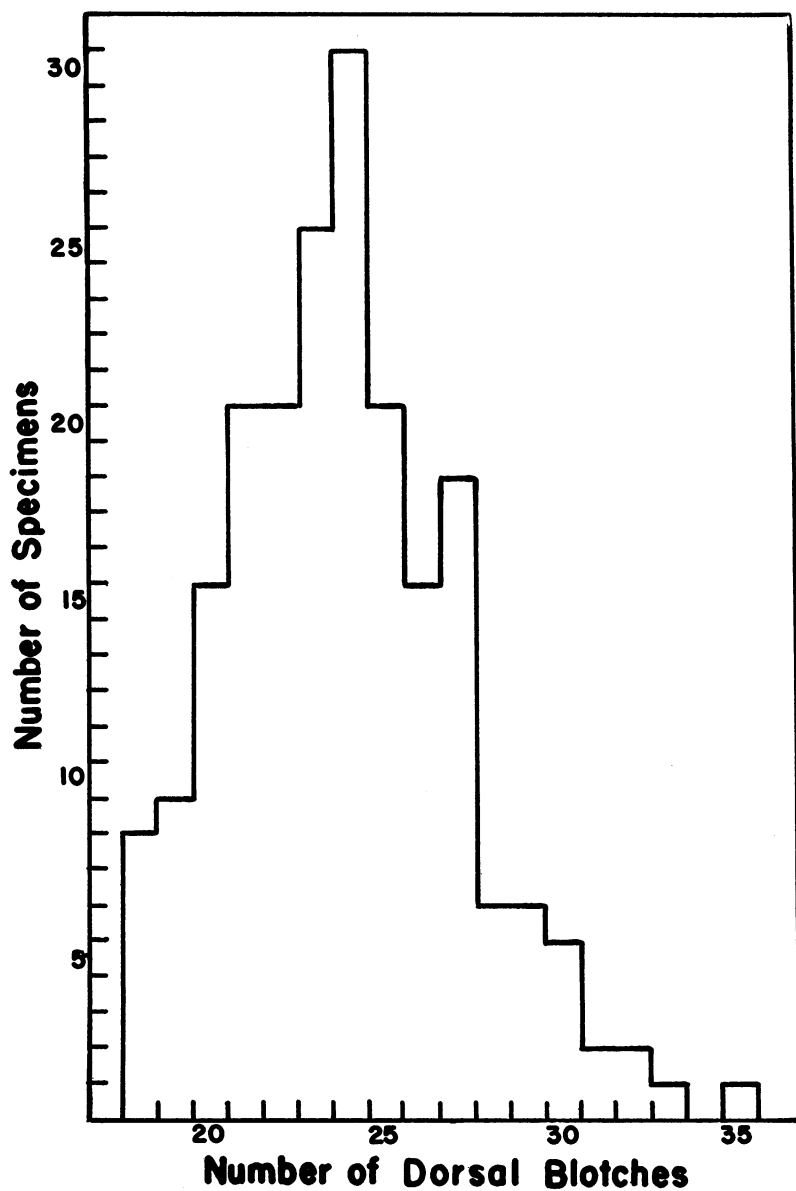


FIG. 18. Histogram showing normal distribution of number of dorsal blotches within a single population, the Iquitos series. The sexes have been combined.

part of a ratio is responsible for the differences seen, there can be little doubt that tail length is the dimorphic half of the fraction and only repeats the dimorphism shown by the subcaudal and the tail blotch counts.

Edgren (1951, p. 1) indicated that the placement of the umbilical scar was dimorphic between the sexes in *Heterodon platyrhinos* Latreille and suggested that "the position of the scar, in terms of ventral plates involved, is about as accurate an index of sex as the ventrals or the caudals." The position of the umbilical scar was recorded for all juveniles of *Dipsas catesbyi* on which it was determinable, and this was true in 39 specimens, including 23 females and 16 males. If the available data for *catesbyi* are analyzed in the same fashion as that used by Edgren, a statistically significant dimorphism can be observed. If, however, the position of the umbilical scar is studied in relationship to a more closely related point of reference such as the anal plate, the dimorphism is no longer so striking as before. The following frequency distribution, set up in part as were Edgren's data, indicates first the dimorphism and then its absence:

ANTERIOR END OF SCAR			VENTRALS FROM ANAL PLATE TO ANTERIOR END OF SCAR		
Ventrals	Females	Males	Ventrals	Females	Males
142-143	1	—	16-17	—	1
144-145	—	—	18-19	2	—
146-147	1	—	20-21	8	1
148-149	1	—	22-23	6	9
150-151	5	—	24-25	4	2
152-153	2	—	26-27	—	1
154-155	5	2	28-29	1	1
156-157	4	—	30-31	1	—
158-159	1	—	32-33	—	—
160-161	—	1	34-35	—	1
162-163	2	4			
164-165	—	5			
166-167	1	2			
168-169	—	2			

If the data in the second and third columns are treated statistically, it is found that the difference between the means for the two sexes is 5.6 times greater than the standard error of the difference, which is a strongly significant value, and serves as a verification of Edgren's results. If, however, the data in the last two columns are compared in the same fashion, it is found that the difference between the means for the two sexes is 1.1 times greater than the standard error of the difference, and is not a significant value. It indicates, therefore, that there is no difference

between the sexes when the character is measured in a slightly different way.

This apparently contradictory situation is primarily a result of choice of point of reference. If the total number of ventrals anterior to the umbilical scar is used, virtually the entire length of the body is included in the analysis. If, on the other hand, the number of ventrals between the scar and the anal plate is used, the distance is quite small, and the dimorphism can be proved absent. This indicates that whatever the source of the dimorphism might be, the area in which it is located is anterior to the umbilical scar. The data indicate that the sexual dimorphism exhibited by both the total ventral counts and the position of the umbilical scar are not the primary facts but are only secondary manifestations of a less obvious difference. Edgren suggests that "the embryological reasons for this apparent dimorphism remain obscure at this time; however, they are probably involved in the ontogenetic production of the differential body proportions between the sexes of snakes." I think it likely that the basis for this dimorphism will prove to be differences in structure rather than proportion, particularly in several of the larger organs.

## SUMMARY AND CONCLUSIONS

The large series of snakes in the Bassler collection of the American Museum of Natural History have made possible thorough analysis of a tropical species of snake and of individual populations within the species. This analysis provides a solid basis for evaluation of species variation within the subfamily Dipsadinae and also for comparison with species of snakes from temperate areas for which similar analyses are available.

Variations in number of upper labials take place on all parts of the labial row, about equally as often anterior to and in the eye, about half that frequently postorbitally. Postorbital variation is comparatively rare in snake species previously studied.

There is considerable geographical discordance between independent characters when analyzed by populations, and it is felt that this discordance negates the value of subspecific designations.

There appears to be an annual growth increment of approximately 50 mm. during the first four years of life, after which age groups cannot be differentiated.

There seems to be no differential growth rate between sexes for this tropical species, although such a dimorphism is commonly observed in temperate (North American) species.

A slightly marked ontogenetic increase in tail length can be demon-

strated and is possibly due to a selective force favoring proportionately longer tails as body weight and length increase.

Observations by earlier authors that adults are less variable than juveniles of the same species have not been borne out by *catesbyi*. With regard to ventral counts, at least, adults are as variable as juveniles.

Sexual dimorphism is greater in subcaudal than in ventral counts and is present in the tail-blotch counts while absent in body-blotch counts. The tail length/body length ratio reflects this greater variability of tail characteristics well.

An apparent sexual dimorphism in the location of the umbilical scar is shown to be of a secondary nature, for the dimorphism is absent if the scar is located with relationship to the anal plate.

## REFERENCES CITED

AMARAL, AFRANIO DO

1926. Ophidios do Matto Grosso. Publ. Com. Linhas Telegr. Estrateg. do Matto Grosso ao Amazonas, no. 84, pp. 1-29.

"1929" [1930]. Estudos sobre ophidios neotropicos, XVIII. Lista remissiva dos ophidios da região neotropica. Mem. Inst. Butantan, vol. 4, pp. 127-128, i-viii, 129-271.

BARBOUR, THOMAS, AND GLADWYN KINGSLEY NOBLE

1920. Amphibians and reptiles from southern Peru collected by the Peruvian expedition of 1914-1915 under the auspices of Yale University and the National Geographic Society. Proc. U. S. Natl. Mus., vol. 58, pp. 609-620.

BERG, CARLOS

1901. Herpetological notes. Comun. Mus. Nac. Buenos Aires, vol. 8, pp. 289-291.

BERGMAN, R. A. M.

1950. The life of *Natrix vittata* (L.). Zool. Meded., vol. 31, pp. 1-11.

BOIE, FRIEDRICH

1827. Bemerkungen über Merrem's Versuch eines Systems der Amphibien. Isis, vol. 20, pp. 508-566.

CARPENTER, CHARLES

1952. Growth and maturity of the three species of *Thamnophis* in Michigan. Copeia, 1952, pp. 237-243.

DUMÉRIL, A. M. C., G. BIBRON, AND A. DUMÉRIL

1854. Erpétologie générale ou histoire naturelle complète des reptiles. Paris, vol. 7, pt. 1, pp. 1-780.

DUNN, EMMETT REID

1942. Survival value of varietal characters in snakes. Amer. Nat., vol. 76, pp. 104-109.

EDGREN, RICHARD

1951. The umbilical scar, a sexually dimorphic character in *Heterodon platyrhinos*. Nat. Hist. Misc., no. 83, pp. 1-2.

FITCH, HENRY S.

1949. Study of snake populations in central California. *Amer. Midland Nat.*, vol. 41, pp. 513-579.

FITCH, HENRY S., AND BEN GLADING

1947. A field study of a rattlesnake population. *California Fish and Game*, vol. 33, pp. 103-123.

GÜNTHER, ALBERT

1858. Catalogue of the colubrine snakes in the collection of the British Museum. London, xvi + 281 pp.

INGER, ROBERT

1943. Further notes on differential selection of variant juvenile snakes. *Amer. Nat.*, vol. 77, pp. 87-90.

KLAUBER, LAURENCE M.

1937. A statistical study of the rattlesnakes, IV. The growth of the rattlesnake. *Occas. Papers San Diego Soc. Nat. Hist.*, no. 3, pp. 1-56.

1943. Tail-length differences in snakes with notes on sexual dimorphism and the coefficient of divergence. *Bull. Zool. Soc. San Diego*, no. 18, pp. 1-60.

OLIVER, JAMES A.

1948. The relationships and zoogeography of the genus *Thalerophis* Oliver. *Bull. Amer. Mus. Nat. Hist.*, vol. 92, pp. 161-280.

PETERS, W.

1871. Mittheilung über eine von Hr. Dr. Robert Abendroth in dem Hochlande von Peru gemachte Sammlung von Amphibien. *Monatsber. Akad. Wiss. Berlin*, pp. 398-404.

SCHMIDT, KARL PATTERSON

1952. The Surinam coral snake, *Micrurus surinamensis*. *Fieldiana, Zool.*, vol. 34, pp. 25-34.

SENTZEN, U. J.

1796. Ophiologische Fragmente, 6. Beschreibung des *Coluber Catesbeji*. *Meyer's Zool. Arch.*, vol. 2, pp. 66-74.

STUART, LAWRENCE C.

1941. Studies of neotropical Colubrinae VIII. A revision of the genus *Dryadophis* Stuart, 1939. *Misc. Publ. Mus. Zool. Univ. Michigan*, no. 49, pp. 1-106.

VAN DER VAART, H. R.

1953. Adult age, an investigation based on certain aspects of growth curves. *Acta Biotheor.*, vol. 10, pp. 139-212.

VANZOLINI, PAULO EMILIO

1951. *Amphisbaena fuliginosa*. *Bull. Mus. Comp. Zool.*, vol. 106, pp. 1-67.

WILSON, EDWARD O., AND WILLIAM L. BROWN, JR.

1953. The subspecies concept and its taxonomic application. *Syst. Zool.*, vol. 2, pp. 97-111.

