

The Frog Genus *Atelopus* in Ecuador
(Anura: Bufonidae)

JAMES A. PETERS

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 145

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SMITHSONIAN INSTITUTION PRESS

City of Washington

1973

ABSTRACT

Peters, James A. The Frog Genus *Atelopus* in Ecuador. *Smithsonian Contributions to Zoology*, number 145, 49 pages, 31 figures, 1973.—The genus *Atelopus* is represented in Ecuador by 15 species, of which 6 are here described as new taxa. A key for identification, descriptions, and figures are presented for all species, and a detailed analysis of variation in proportions attempts to quantify certain subjective characteristics used by earlier frog systematists.

The genus includes two nonphylogenetic groups of species, the first, with slender bodies and long limbs, usually found in the lowlands and lower mountain slopes, and the second, with stocky bodies and short limbs, usually found at higher altitudes in the Andes. The species appear to be highly responsive to environmental changes, and successful invasions of the mountains by the lowland species are accompanied by differentiation, evolution, and speciation. Invasions are likely to be along major river drainages. The invaders are effectively isolated from adjacent drainages by factors such as the highly dissected terrain, rain shadow, barren areas, and so on. High altitude species are restricted in lateral distribution, but often have considerable altitudinal range, while low altitude species have wide latitudinal range, but are restricted altitudinally.

The mountains in Ecuador are "continental islands," showing diversity and adaptive radiation similar to that of the Hawaiian Islands, with the major difference that the Andes are not dependent upon "waifs" or "drifters" for invaders, but are constantly supplied by the abundant life of the surrounding tropical forests.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SI PRESS NUMBER 4775. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data

Peters, James Arthur, 1922-1972

The frog genus *Atelopus* in Ecuador.

(Smithsonian contributions to zoology, no. 145)

Bibliography: p.

1. *Atelopus*. 2. Frogs—Ecuador. I. Title. II. Series: Smithsonian Institution. Smithsonian contributions to zoology, no. 145.

QL1.S54 no. 145 [QL668.E2] 591'.08s [597'.8] 72-13540

For sale by the Superintendent of Documents,
U.S. Government Printing Office, Washington, D.C. 20402
Price 85 cents, domestic postpaid; 60 cents, GPO Bookstore

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The Frog Genus *Atelopus* in Ecuador (Anura: Bufonidae)

James A. Peters

Introduction

It has been my good fortune to be able to spend considerable time in the field in Ecuador, where I collected representatives of most of the species of *Atelopus* now known from that country. There are three new species in the material I obtained, and three more new species have been identified in the collections of other museums. In addition, the taxonomic position of several of the previously described forms has been revised as a consequence both of the new material available and of reexamination of the type specimens or series. The preparation of this paper has been stimulated by the recent work on the genus *Atelopus* by Juan Rivero. My collections strongly supplement his material, and I have found his discussions of the Ecuadorian species cogent and stimulating, even with regard to those points on which we are not in agreement.

The synonymies presented for each species are limited to only those references pertaining to Ecuadorian records and specimens, except where a change in status of the taxon is involved. I have made no attempt to document use of a taxonomic name in an inclusive manner.

ACKNOWLEDGMENTS.—My field work in Ecuador was supported in 1954 by the American Philosophical Society and Brown University, in 1962 by Grant No. G21010 of the National Science Foundation, and in 1965–1966 by the Smithsonian Institution. I am indebted to each for this aid. Many people

have helped me to amass the material on which this study is primarily based, and I wish particularly to thank Manuel Olalla, Peter Spoecker, Robert Mullen, and Gonzalo Herrera, who have helped in the field. Gustavo Orcés-V. continues as an invaluable friend and critic, and his collections, now at the National Museum of Natural History, Smithsonian Institution, were extremely useful in this study. The curators at the following institutions have loaned specimens to me and have provided me with space to work during visits to their institutions, and I appreciate both kindnesses (abbreviations used in the text follow the name): American Museum of Natural History (AMNH); British Museum (Natural History) (BMNH); California Academy of Sciences (CAS, CAS-SU refers to numbers assigned to specimens from the collections of Stanford University, now housed at the Academy); Field Museum of Natural History (FMNH); Museo ed Instituto di Zoologia Systematica, Università di Torino, Italy (UT); Museo Nacional de Ciencias Naturales, Madrid, Spain (MM); Museum of Comparative Zoology, Harvard University (MCZ); Muséum National d'Histoire Naturelle, Paris, France (PM); University of Kansas Museum of Natural History (UKMNH); University of Michigan Museum of Zoology (UMMZ); and University of Puerto Rico, Mayaguez (UPR-M). The abbreviation used for the collections in the National Museum of Natural History is USNM (United States National Museum). Uncataloged specimens from the James A. Peters (JAP) and the Gustavo Orcés-V. (GOV) collections are deposited at the National Museum of Natural History.

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SPECIES GROUPS WITHIN THE GENUS.—Although one should not attempt the definition of species groups unless his study encompasses the entire range of variation in the genus, it has been most convenient for me to recognize that there are two different groups of species in the Ecuadorian *Ateolopus*. I am not here according these groups any kind of taxonomic status, and I regard them as phenetic rather than phylogenetic, so I would not like to have any taxonomic or phylogenetic interpretation placed on my treatment of them. But the groups do provide an evident basis for discussion and organization of data, as well as a primary step in definition of the species and in the preparation of a key for identification.

The *longirostris* group includes the slim-bodied, long-legged taxa, while the *ignescens* group includes the taxa with short, heavy-set bodies and short limbs. Brighter colors and flash patterns tend to occur more commonly in the *longirostris* group, while the members of the *ignescens* group tend to have darker, more sombre colors. Coloration is not invariable, however, and is not a good basis for group recognition. The *longirostris* group is found at lower altitudes on both sides of the Andes in Ecuador, while most of the taxa in the *ignescens* group are high altitude forms.

The species in the *ignescens* group include *arthuri*, *bomolochos*, *bufoniformis*, *halihelos*, *ignescens*, *nepiozomus*, and *pachydermus*. The members of the *longirostris* group are *balios*, *elegans*, *longirostris*, *palmatius*, *planispinus*, and *pulcher*. The largest species of all, *boulengeri*, and one of the smallest, *mindoensis*, are intermediate between the two groups in many respects, and are difficult to assign in any unequivocal way. This intermediacy is referred to repeatedly in the subsequent sections, and reinforces my statement above that these are not taxonomic groupings, but simply represent convenient groupings. The species are arranged on the graphs in the following sections by groups, with the two "intermediate" species between them.

While groups were not emphasized as such by McDiarmid (1971) in his recent review of the genus, and he repeatedly pointed out the uniformity of characters within *Ateolopus* in contrast to its differences when compared with other genera, he did recognize the existence of the two groups discussed here. He referred in several places to

the long-legged and the short-legged species, and pointed out several anatomical characteristics which differentiate the two groups. Unfortunately, his samples were not large enough to permit full review of all the Ecuadorian species. Where he had material it was usually only a single specimen, and he had no material at all for several of the taxa.

COMPARATIVE MEASUREMENTS.—All measurements used in this study were made with a Helios vernier caliper, measuring to the nearest tenth of a millimeter. The "standard distance" is the straight-line distance between the tip of the snout and the posterior end of the coccyx. Although many previous authors have defined the body length as from the snout to the anus, preservation techniques have an effect on the position of the anus, and the tissues in that region can be easily compressed, so the measurement is more variable and not as accurate or consistent as the one defined here. All other measurements are taken from a bony surface to another bony surface, insofar as possible. The measurement from knee to knee is made with the femora at right angles to the body, forming a straight line. The calipers are set solidly against the distal ends of the femora to record the measurement. The tibiofibula measurement is from end to end of the bone. The head width is taken at the widest point of the head, with the points of the caliper set to pass snugly over the head. The head length is from the snout tip to the posteriormost margin of the skull at the dorsal midline.

As mentioned elsewhere, the two species groups are clearly distinctive in their general appearance. The differences are well reflected by calculations of proportional values, using the various measurements discussed above. In some proportions there is a considerable sexual dimorphism, and the sexes are separated in all calculations, even where the differences were not significant.

The figures show the mean as a vertical line, the total range of variation as the largest rectangle, the mean \pm twice the standard error of the mean as the smallest rectangle, and the mean \pm one standard deviation as the third rectangle. Only the mean and range are given for very small samples (fewer than 6). The colors of the rectangles are reversed from one sex to the other to permit rapid recognition. The value found as a proportion is

always plotted in these figures as a percentage, and it should be clear that all references to ratios, proportions, and percentages are to these figures.

All references in this paper to significant differences between the means of any two samples is based on non-overlap between the rectangles representing the mean \pm twice its standard error. This spread of values includes slightly more than 95 percent of the possible values of the mean itself, and nonoverlap between the two populations indicates a very high likelihood that the two samples as drawn are different.

Ratio

KNEE TO KNEE/STANDARD DISTANCE.—In this ratio, seen in Figures 1 and 2, higher values indicate a longer leg in proportion to body length, or standard distance. Although the two species groups are quite distinct from each other both in body shape and leg length, as pointed out elsewhere, this is not strongly reflected by proportional differences. This is because both body and legs are elongated in the *longirostris* group, while in the *ignescens* group both body and legs are short and stubby.

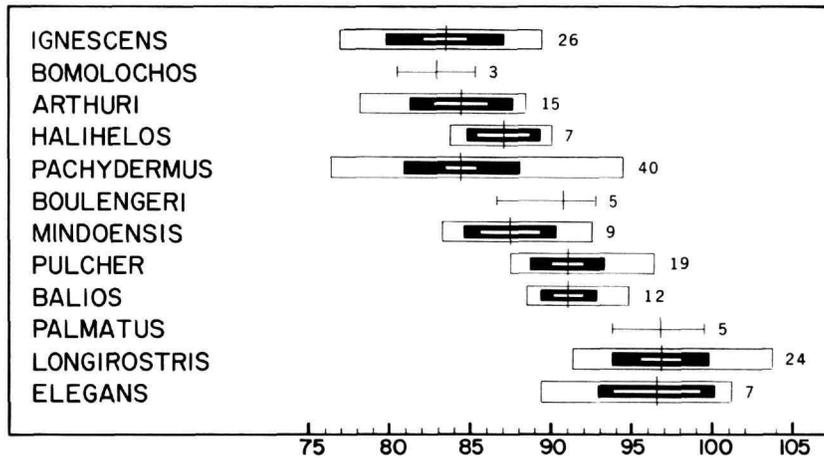


FIGURE 1.—Species comparison, males, for the ratio knee to knee/standard distance \times 100. Numbers in this and Figure 2 refer to sample size, which are same for other figures.

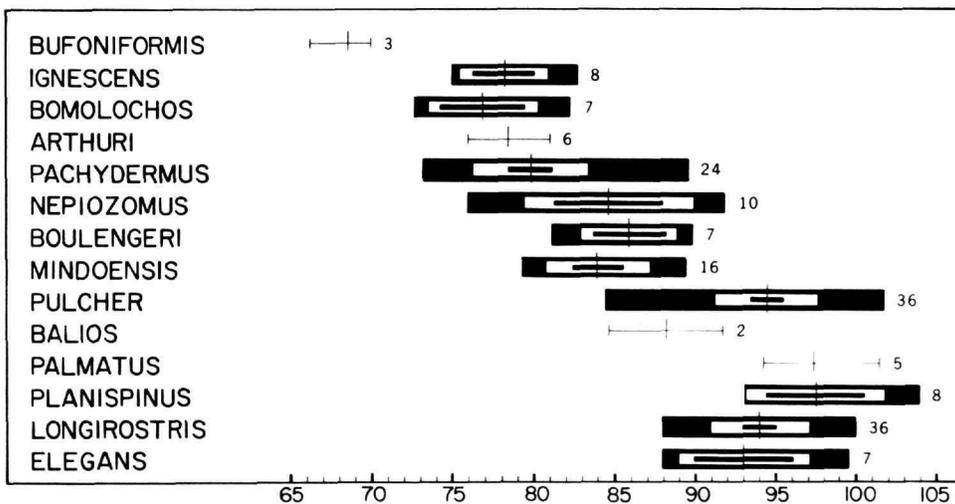


FIGURE 2.—Species comparison, females, for the ratio knee to knee/standard distance \times 100.

Even so, the *longirostris* group is characterized by values greater than 89 for the proportion, while individual proportions in the *ignescens* group are almost always below 90. *A. pachydermus* males, of the *ignescens* group, range up to values of 94, and *A. balios*, of the *longirostris* group, has values for most of the females and many of the males below a ratio of 90. *A. mindoensis* and *A. bouleengeri* are fairly typical of the *ignescens* group, with only a few males falling above a value of 90.

Sexual dimorphism is fairly strong in this characteristic. There is a significant difference between the means for the sexes in every species except *A. elegans*, when samples are large enough for comparison, although there is considerable overlap in

the range of variation of the sexes. The males have longer legs in proportion to the body length than the females in every species.

TIBIOFIBULA/STANDARD DISTANCE.—This character is similar to the previous one (KK/SD) in that it is an expression of a primary difference between the two groups of species, but it expresses the contrast much more strongly (Figures 3 and 4). Although the body and femora have changed in such a fashion that the proportion between them is similar in the two groups, the region of the tibiofibula is much more elongated, proportionately, than the femoral region in the *longirostris* group, and this has been reflected in this ratio.

Individuals in the *ignescens* group are characterized by values below 45 for this ratio, while

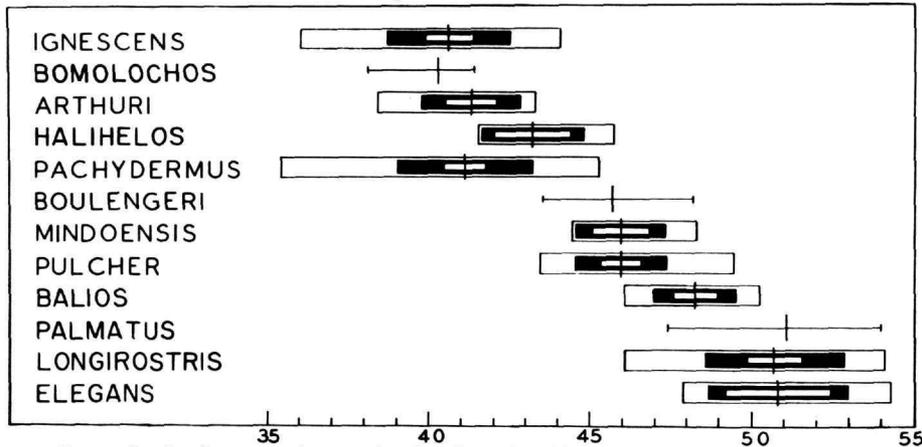


FIGURE 3.—Species comparison, males, for the ratio tibiofibula/standard distance $\times 100$.

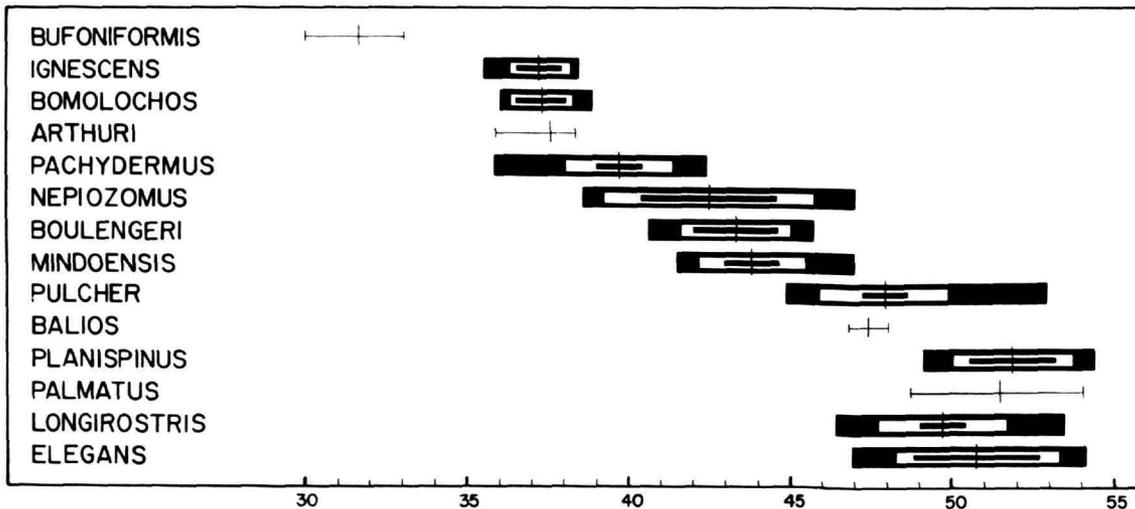


FIGURE 4.—Species comparison, females, for the ratio tibiofibula/standard distance $\times 100$.

those in the *longirostris* group almost invariably have values above 45. In the latter group only males and females of *A. pulcher* give lower figures, while the remaining species have practically no individuals with values below 46. In the *ignescens* group males of *A. pachydermus* and *A. halihelos* include individuals with values above 45, none of which reach 46, and females of *A. nepiozomus* may have values up to 47. No males of *A. nepiozomus* have yet been taken, but it might be predicted that they would give higher values, as well.

The two species *A. mindoensis* and *A. bouleengeri* are completely intermediate in this character. Most of the females of both species lie below 46, most of the males of both fall above 45. Within the sexes, the mean for each of these species is significantly higher than that of all others within the *ignescens* group, except for females of *A. nepiozomus*, but the same is true of a comparison with the members of the *longirostris* group, where the values for these two species are significantly lower.

Sexual dimorphism is apparent in all species of the *ignescens* group for this character, with the males having means significantly higher than the females. The opposite is true of the *longirostris*

group, for in no case are the means of the two sexes significantly different. In this regard, *A. mindoensis* and *A. bouleengeri* show similarities to the *ignescens* group, since the means for the sexes are significantly different in both species.

HEAD LENGTH/STANDARD DISTANCE.—This ratio (Figures 5 and 6) produces differences between species within the two major groups, rather than

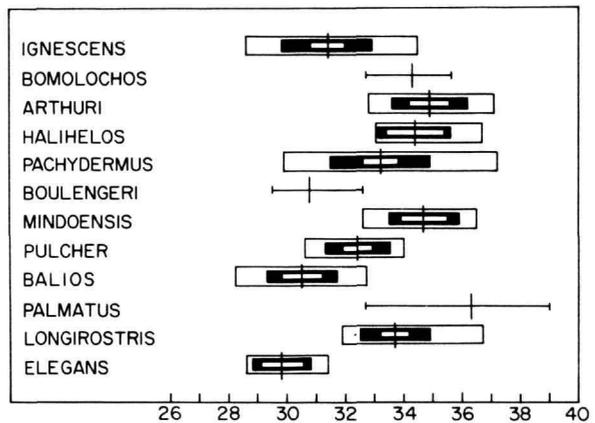


FIGURE 5.—Species comparison, males, for the ratio head length/standard distance $\times 100$.

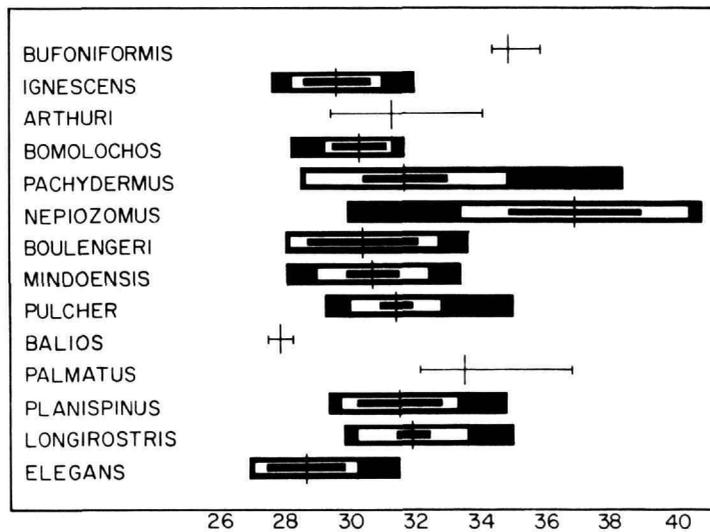


FIGURE 6.—Species comparison, females, for the ratio head length/standard distance $\times 100$.

following group lines, and thus provides a basis for separation of species within groups. Thus, all individuals of *A. balios* and *A. elegans*, both of the *longirostris* group, fall below a proportional value of 33, as do the following species from the *ignescens* group: all females of *A. bomolochos* and *A. ignescens* and all males of *boulengeri*. In the *longirostris* group this is also true of most individuals of both sexes of *A. pulcher* as well as females of *A. planispinis* and *A. longirostris*, and in the *ignescens* group, most of the males of *A. ignescens* as well as the females of *A. arthuri*, *A. boulengeri*, and *A. mindoensis*. On the other hand, values of greater than 33 are found, in the *ignescens* group, in all *A. bufoniformis* as well as the males of *A. arthuri*, *A. mindoensis*, *A. halihelos*, and *A. bomolochos*, while, in the *longirostris* group, values above 33 are characteristic of both sexes of *A. palmatus*, and the females of *A. longirostris*. *A. pachydermus*, of the *ignescens* group, is completely intermediate in this character, with as many individuals in both sexes with values above 33 as those below. The mean for females in this species is 31.7, for males it is 33.2.

It is apparent from the figures above that sexual dimorphism occurs in some of the species, but again it is a mixture between groups. In the *ignescens* group significant differences exist between the means for the sexes in *A. bomolochos*, *A. arthuri*, and *A. mindoensis*, while there are no sexual dif-

ferences within *A. boulengeri* or *A. pachydermus*, and the means for the sexes in *A. ignescens* are very narrowly different at the 95 percent level. In the *longirostris* group, significant sexual differences in this character exist in *A. longirostris* at a high level of significance, and in *A. pulcher* with only marginal significance, but not at all in *A. elegans*. It appears likely that sexual dimorphism exists in *A. balios*, and perhaps not in *A. palmatus*, but the samples are insufficient to be certain of either.

HEAD WIDTH/HEAD LENGTH.—As seen in Figures 7 and 8, the members of the *ignescens* group are characterized by a broad head in relation to its length (measured from the tip of the snout to the posteriormost point on the dorsal midline). This is most exaggerated in *A. ignescens* itself. The distinction between the two groups is not sharp, and several species show an intermediate condition. Within the *ignescens* group, *A. bufoniformis*, *A. ignescens*, *A. arthuri*, *A. pachydermus*, and *A. boulengeri* are quite distinct, with all the individuals showing a ratio of 95 or more. Also, within the *longirostris* group, *A. planispinus*, *A. palmatus*, and *A. longirostris* are equally distinct, with ratios generally below 92. Three species in the *ignescens* group also show such low values, however, including *A. bomolochos*, *A. halihelos*, and *A. nepiozomus*, with the means for the last two significantly different from all other species in the group, and with the latter two having mean values below 90.

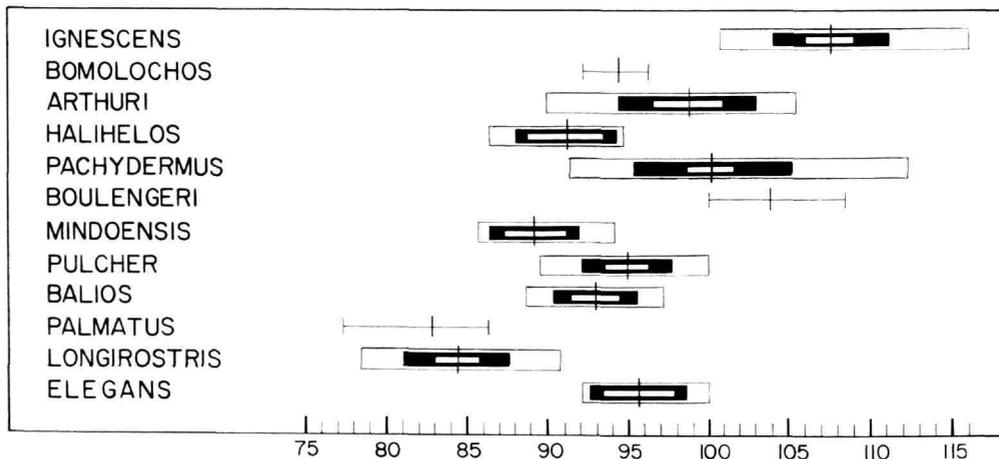


FIGURE 7.—Species comparison, males, for the ratio head width/head length $\times 100$.

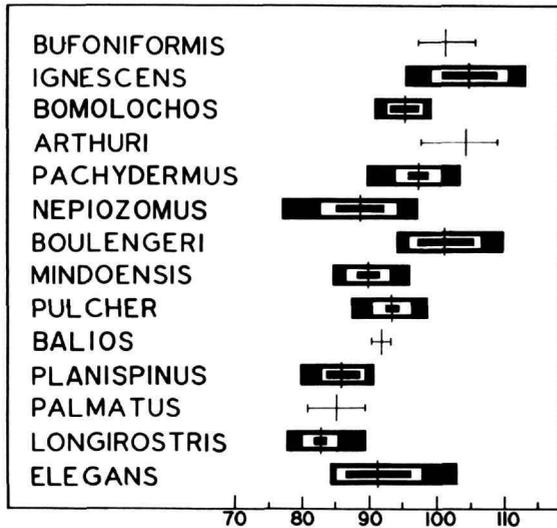


FIGURE 8.—Species comparison, females, for the ratio head width/head length $\times 100$.

In the *longirostris* group, *A. pulcher*, *A. balios*, and *A. elegans* all have higher ratios, indicating proportionately broader heads.

There are no species with differences between the means for the sexes that are statistically significant, i.e., no sexual dimorphism exists in this character.

TIBIOFIBULA/HEAD LENGTH.—This ratio, as shown in Figures 9 and 10, demonstrates the dichotomy of the two groups, and the intermediacy of *A. mindoensis*. Members of the *ignescens* group generally have proportional values below 135, and

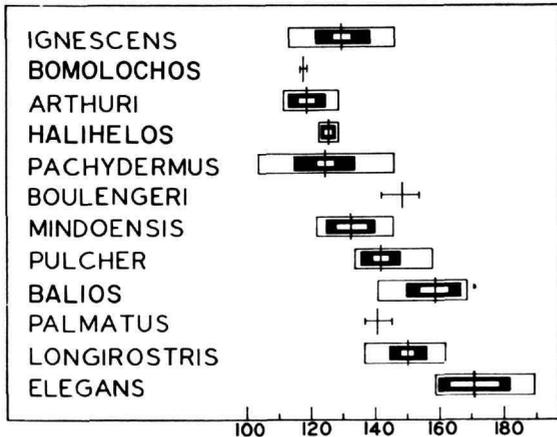


FIGURE 9.—Species comparison, males, for the ratio tibiofibula/head length $\times 100$.

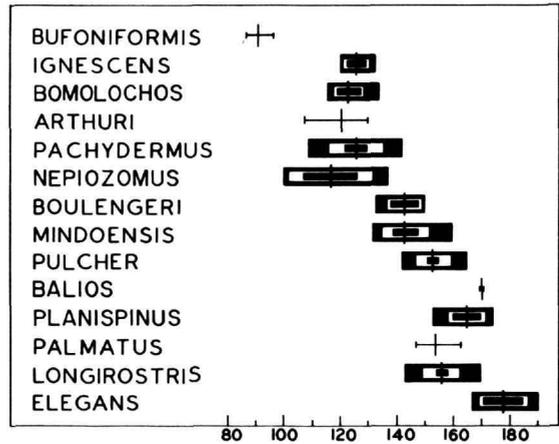


FIGURE 10.—Species comparison, females, for the ratio tibiofibula/head length $\times 100$.

those of the *longirostris* group are generally above 135. *A. bufoniformis* is very distinct, overlapping only one other species in its total range of variation.

In those species for which there are sufficient individuals of both sexes for comparison, there is no sexual dimorphism in the *ignescens* group, with the exception of *A. mindoensis*. In this regard *A. mindoensis* is more like the species of the *longirostris* group, where a significant difference between the means for the two sexes occurs in all species except *A. elegans*.

TIBIOFIBULA/KNEE TO KNEE.—This ratio (Figures 11 and 12) is an attempt to express quantitatively a relationship often used in the earlier litera-

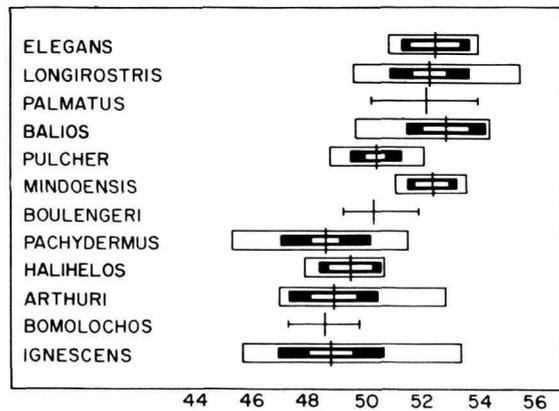


FIGURE 11.—Species comparison, males, for the ratio tibiofibula/knee to knee $\times 100$.

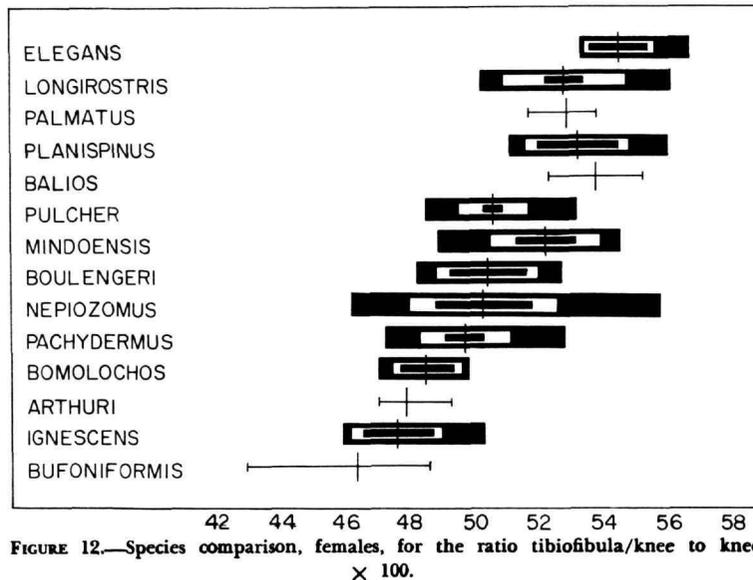


FIGURE 12.—Species comparison, females, for the ratio tibiofibula/knee to knee $\times 100$.

ture on anuran taxonomy. The lower limb is placed parallel to the femur, which is extended at right angles to the body, and the relationship of the heels in this position is usually stated as overlapping, touching, or separated. Quantitatively, if the heels overlap, the value of this ratio is usually greater than 51, while if the heels are separated, it is smaller than about 50. Most of the members of the *ignescens* group give values below 50, while the species in the *longirostris* group usually show ratios above 51. *A. bufoniformis* shows the lowest values of the genus in Ecuador. *A. mindoensis* diverges sharply from the *ignescens* group in this characteristic, with all the males having ratios higher than 51, and only 2 of the 16 females with ratios below 51. *A. boulengeri* is intermediate, with values ranging from 48 to 52 in both sexes, although in every case in this species the heels do not overlap, as a consequence of the method of measurement.

Although the two principal groups are distinguishable, and the means for this character are significantly different between species of the groups, the ranges of variation often overlap extensively, and this is not a good character for population and species differentiation. It appears that the proportional relationships between these two parts of the hind leg remain rather constant, even though in the *ignescens* group the leg is short, stubby, and

muscular, while in the *longirostris* group the leg is long, lean, and slender.

Sexual Dimorphism

In addition to the several characteristics discussed under the heading of comparative measurements, there are other cases of distinctive sexual dimorphism in Ecuadorian *Atelopus*. The most conspicuous sexual difference is associated with the act of clasping, which in this genus is a matter of some magnitude, in light of the length of time that the clasp is maintained. Males of most species have a cornified edge on the first digit of the forefoot, and in several species this cornified area is expanded well onto the second digit and adjacent areas of the palmar surface. This horny area permits external sex determination in almost every case, since it is never present in females. The amount of cornified tissue is considerably greater than in most anuran species, and is presumably very useful to the male in the maintenance of his tenacious grip on the female while awaiting the deposition of the eggs. Since amplexing pairs may remain that way for as long as two weeks (see "Remarks" under *A. ignescens*), a good grip is rather important.

Rivero (1963:109) has remarked, "Spiny or tubercular skin is apparently not a sexual character

in *Atelopus*, although in tubercular species, the male is usually more distinctly so than the female." This has not been true in the species I have examined, for all species with tubercles show considerable sexual dimorphism in the number, distribution, and prominence of warts, tubercles, and particularly in spiny points, single or several, on the tops of the warts or glandular areas. In

each case it is the female that is more heavily warty or densely spinose, quite the reverse of the situation in related amphibians, including other genera in the Bufonidae. In some Ecuadorian species, the males are almost smooth on the sides of the body and the temporal region, while the females have prominent spines in the same area.

Key to the *Atelopus* of Ecuador

1. Legs long, thin; body usually slender; heels overlap or touch when tibiofibulae are parallel to femora at right angles to body; ratio tibiofibula/SD usually more than 45.....2
 Legs short, stout; body stout; heels do not touch when tibiofibulae are parallel to femora at right angles to body; ratio tibiofibula/SD usually below 45.....9
2. First finger almost entirely hidden in webbing; tip may be free3
 First finger distinct; webbing somewhat incised between first and second fingers6
3. Belly unicolor, without spotting4
 Belly with clear-cut, marked, round black spots..... *pulcher*
4. Dorsum whitish with irregularly parallel, broad, black or brown stripes *elegans*
 Dorsum not colored as above5
5. Dorsum with broad band of light yellowish brown, filled with reddish brown marbling and spotting *mindoensis*
 Dorsum chocolate brown, dorsolateral streak and dorsal spotting of light gray, bordered by narrow brown or black edge *palmatum*
6. Limbs smooth7
 Limbs not smooth; may be shagreened, pustulate or warty8
7. Ground color of dorsum of body light tan, with many small, rounded, regular darker brown spots *balios*
 Ground color of dorsum dark brown, with small, light yellowish spots often bilaterally symmetrical *longirostris*
8. Entire body and limbs light brown, with small, scattered, dark spots above and below
halihelos
 Dorsum light tan, vermiculated with light to dark brown, venter yellowish white, no spotting *planispinus*
9. First finger distinct, free at least in part from webbing10
 First finger indistinct, entirely enclosed in webbing..... *bufoniformis*
10. Areas of spinules, warts, or pustules on some parts of head and/or body, usually on sides and temporal region11
 Skin of head and body entirely smooth, no pustules, warts, or spinules..... *boulengeri*
11. Dorsum not unicolor, or, if so, not black12
 Dorsum unicolor, usually black, color extending well down sides and onto venter .. *ignescens*
12. Dorsum with strongly contrasting light (white or yellow) and dark (usually black) areas, legs dark brown to black, usually with yellow spotting *pachydermus*
 Dorsum not as described13
13. Middorsum yellowish or greenish, with few scattered dark spots or uniform; no pustules or warts on humerus, tibiofibula, or tarsometatarsus; dorsum of body usually smooth, but few individuals have low warts posteriorly.....14
 Color not as described; all parts of limbs usually with warts, pustules, or spinules; dorsum may or may not be warty15
14. Humerus smooth, no pustules or glandular areas; ratio head length/SD \times 100 greater than 33 *bomolochos*
 Humerus pustulate in females, with small rounded glands in males; ratio HL/SD \times 100 smaller than 33 *ignescens*
15. Middorsum of body with many low, rounded warts, which may have one to many whitish spicules on them, venter usually dark brown with scattered darker spots..... *nepiozomus*
 Middorsum of body smooth, no warts or pustules; venter yellow, without spots (bright red in life) *arthuri*

The males are smaller than the females in those species where both sexes have been taken. The forelimb of the male is stouter and more muscular than in the female, presumably also associated with the mating behavior, at least as observed in *A. ignescens* (see elsewhere). The humeral area of the forearm is usually noticeably thinner than the radioulna area, which is quite thick. As a result the males have arms reminiscent of the cartoon character Popeye the Sailor.

Atelopus arthuri, new species

FIGURE 13

HOLOTYPE.—USNM 193470, female, from 15 kilometers north of Pallatanga, Chimborazo Province, Ecuador, at an altitude between 2800 and 2860 meters, collected by Arthur J. Peters, February 14, 1959.

DIAGNOSIS.—A member of the *ignescens* group of Ecuadorian *Atelopus*, with a vermiculate dorsal pattern of light brown and dark brown on both body and limbs; belly clear yellow (tomato red in life) with a brown patch on buttocks and brownish

spotting or vermiculation on chin and throat in some individuals.

DESCRIPTION.—Snout from above with pointed tip; distinct angle in canthus at level of nostril, canthus forms straight line angled outward from nostril to eye; snout, canthus, and upper eyelid heavily fleshy and raised, with continuous fleshy fold from posterior corner of eye to back of head. Muzzle between canthi distinctly concave, rest of dorsum of head flat. Snout from side distinctly protruding beyond upper lip and lower jaw, nostril directed laterally and slightly posteriorly; loreal region vertical anteriorly, distinctly concave immediately before eye; temporal and tympanic areas glandular and pustulate. Dorsum of body quite smooth or finely wrinkled, without pustules; sides of body and most of upper surfaces of limbs heavily pustulate; females with whitish spinules singly or in clusters on top of pustules. Ventral surfaces of body, chin, and limbs smooth or with very fine wrinkles, no or very few pustules.

Forelimb very short; if pulled back along body, tip of longest finger does not reach vent. Forearm slightly larger in diameter than humeral region. Forefoot fleshy, with fleshiness extending into web,



FIGURE 13.—Holotype, USNM 193470, of *A. arthuri*, new species.

which thus appears reduced, although actually including first phalanx of each digit; three phalanges of third and fourth digits are free of web. No tubercles on ventral surface of forefoot in most individuals; some have series of fleshy swellings both sub- and interarticular. Palmar tubercle large, low, rounded; plantar tubercle very weakly defined.

Hind limb short, fleshy; when brought forward along body heel may reach to points between posterior margin of head and axilla. Heels are well separated when tibiofibulae are parallel to femora at right angles to body. Foot with fleshy web, extending to tip of toe on all except fourth digit; deeply incised between digits. Sole of foot smooth, with poorly defined subarticular tubercles; outer metatarsal tubercle smaller than inner, but raised higher, making it more prominent; inner metatarsal tubercle flattened.

COLOR IN ALCOHOL.—Dorsum light grayish brown with darker brown spotting, vermiculation, or streaking; canthus, margin of eye, and parotid swelling usually unicolor grayish brown (in some individuals almost entire head is unicolor). Dorsum of limbs and feet as body, with same light and dark vermiculations, except in some individuals, which show clear, almost colorless, slightly yellow areas on first two digits and webbing of both fore and hind feet. Sides of body as dorsum, with tops of pustules appearing as white spots in some individuals. Chest, belly, and ventral surfaces of thighs and humerus light yellow, with viscera and/or eggs showing through the skin in many individuals. A more or less enlarged brown patch on the thighs below the anus, extending onto ventral surface for short distance. Chin and throat yellow, almost always vermiculate or spotted with dark brown, extending onto girdle region. Ventral surfaces of forearm, crus, and ankle areas of limbs dark brown, occasionally punctate with yellow. Ventral surfaces of digits entirely yellow, with palm and sole also yellow in some individuals. When palm and sole are partly or wholly brown, tubercles are yellow topped and contrast strongly with brown areas. One individual (USNM 193466) has a reddish brown venter rather than yellow.

COLOR IN LIFE.—Ground color of dorsum dark brown, heavily reticulate with orange-yellow. Ground color on sides dull reddish orange, with dark brown reticulations. Large tomato-red spot ventrally, on thighs, belly, and chest, entirely sur-

rounded by a bright light green, which also covers much of the ventral surfaces of arms and legs. Dorsum of limbs usually as back, joints light orange. Large metatarsal tubercle on outer edge of foot bright yellow, lower surfaces of digits dull orange, as is same surface of forefoot. Pupil black, bright green ring around it, iris black with minute green punctulations.

HOLOTYPE.—The holotype agrees with the description above in all characteristics for which no variation is described. Where the species is variable, the holotype has the following characteristics: skin on dorsum of body wrinkled in nuchal region, smooth on rest of back. Pustules on sides of body and limbs with lighter areas, not clearly spinulate. Ventral surfaces of body wrinkled, a few pustules on throat. Scattered fleshy pustules on ventral surface of forefoot. Plantar tubercle not recognizable. Heel reaches to level of axilla. Subarticular tubercles on hind foot somewhat more prominent than in other individuals. Head with brown vermiculations and spotting. No distinctive colorless areas on feet. Palm yellow, sole brown, with lighter tubercles. Measurements (in millimeters): snout to vent, 46.9; snout to end of coccyx, 40.4; knee to knee, 32.3; tibiofibula, 15.5; head length, 12.5; head width, 12.8; eye diameter, 3.0; snout to eye, 5.9; interorbital distance, 3.5; width of eyelid, 3.5.

VARIATION.—Since the entire type series was collected by my son and me, we were able to gather notes on the variation of the species in life. Individuals are extremely variable in the distribution of the colors of the ventral surfaces, which are tomato red and bright green. One or two have the dorsum almost totally green, with little or no vermiculation. Others have more yellowish orange on the back than dark brown. In addition, individuals may have different colors than the majority, or different distribution of colors and pattern. One or more individuals were taken with the following variants: orange belly and flash areas; green spots on chest, belly, and chin; entire venter green; dark brown stripe or chevron across sternum; greenish yellow reticulations on dorsum; bright green dorsolateral line from eye to groin or from tip of snout to groin; and dorsum of feet green.

ECOLOGY.—The entire type series was collected on February 14 and 15, 1959, at altitudes between 2800 and 2860 meters. The rainy season was late

during that year in that part of Ecuador, and the frogs were actively breeding. Several mated pairs were taken. The species is entirely diurnal, and individuals were found wandering about over quite dry terrain, using a slow walk and hopping only when disturbed. The establishment of pairs appears to be entirely on a visual basis, and there is no calling or chorus on the part of the exploring males. The latter will raise themselves up high on the forelimbs to look about for a female. Mated pairs were found in pools formed in a fairly rapidly flowing mountain stream, but no egg deposition was observed. The voice in the species is characteristic of Ecuadorian *Atelopus* where known, which is a low, chicklike peep, often not distinguishable at any distance. Occasionally males of this species will trill the peep slightly.

ETYMOLOGY.—The species name is derived from the first name of the collector of the holotype, who provided me with pleasant company on the long trip to Papallacta and back, and who collected the first specimens of the new taxon while I was busy fixing our supper.

SPECIMENS EXAMINED.—The following are paratypes: ECUADOR: Chimborazo Province, 15 km N of Pallatanga, between 2800 and 2860 m altitude (AMNH 79461, UKMNH 108938–39, UMMZ 131683, CAS 134199, MCZ 84199, USNM 193463–69, 193471–75).

Atelopus balios, new species

FIGURE 14

A. [atelopus] longibrachius.—Rivero, 1968:22.

A. [atelopus] spurrelli.—Rivero, 1968:22.

HOLOTYPE.—AMNH 17638, female, from the Río Pescado, Guayas Province, Ecuador, collected by G. H. H. Tate, May 28, 1922.

DIAGNOSIS.—A member of the *longirostris* group, with long, thin legs and with heels overlapping when tibiofibulae are parallel to femora at right angles to body; first digit on forefoot distinct, not hidden in webbing; limbs smooth. Similar to *longirostris*, but differs in having a lighter ground color with darker spotting, while *longirostris* has a dark ground color with yellowish spots.

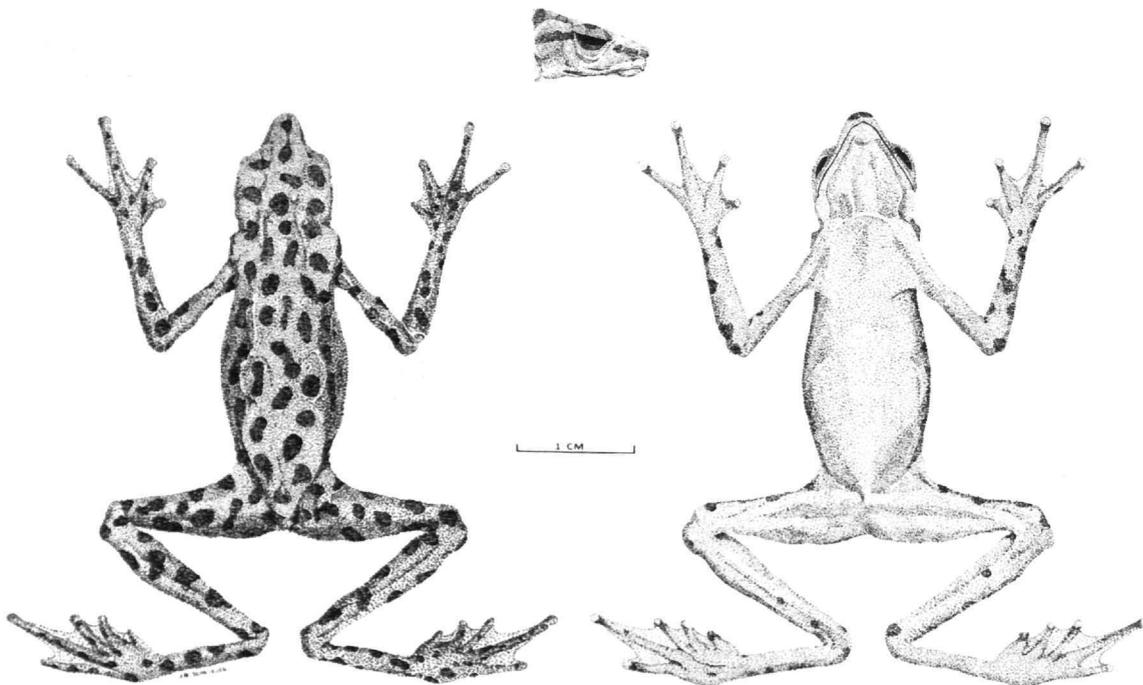


FIGURE 14.—Holotype, AMNH 17638, of *A. balios*, new species.

DESCRIPTION.—Snout from above rounded or with blunt point; outward curve of muzzle becoming inward curve from level of nostril to eye; snout, canthus, upper eyelid, and temporal region somewhat fleshy. Dorsum of snout weakly concave, rest of dorsum of head flat, lightly shagreened. Eye slightly bulging dorsally. Snout from side protrusive over lower jaw and upper lip, forming blunt point; nostril lateral, loreal region vertical or very slightly concave. Eye slightly overhung by fleshy margin of upper eyelid; temporal region more heavily shagreened than dorsum, and also heavily wrinkled. Dorsum almost smooth, very finely wrinkled; sides with wrinkles forming deep creases; chin and belly so heavily wrinkled that areas between wrinkles look like pustules.

Forelimb very slender, with forearm more fleshy than humeral region, dorsum thickly shagreened, ventral area wrinkled. When forearm is pulled back along body, second and fourth digits reach vent. Sole of forefoot fleshy, fleshy webbing encloses all but tip of first digit, extends as fringe to ends of other digits, giving them a flattened appearance, webbing between toes incised to a point about one quarter of distance to digit tips. All subarticular tubercles almost totally indistinguishable, as are both plantar and palmar tubercles, with latter occasionally forming low rounded hump. Males with horny excrescence on first digit of forefoot.

Hind limb slender, finely but densely shagreened dorsally, less dense laterally, giving way to wrinkling on ventral surface. Tibiotarsal articulation may reach to points between anterior edge of eye and anterior margin of tympanic area when carried forward along body. Heels touch or overlap when tibiofibulae are parallel to femora at right angles to body. Entire foot fleshy with thick webbing to tips of toes, first three toes almost totally obscured by webbing, which forms fringe on fourth toe from level of tip of third and fifth toes. No subarticular tubercles, very reduced outer metatarsal tubercle, almost indistinguishable in some individuals, no inner metatarsal tubercle.

COLOR IN ALCOHOL.—Dorsal ground color very light tan, with numerous rounded spots, completely separated from each other. Dorsum of legs, sides of body as dorsum of body, side of head with dark brown line from tip of snout through eye along side of head to shoulder, line either continuous or

irregularly broken into spots along lower sides. Upper lip light, rest of body below stripe usually unicolor light yellowish white, a few individuals with scattered spots on belly. Ventral surfaces of limbs yellowish white, of feet dull yellow.

HOLOTYPE.—The holotype agrees with the description above in all characteristics for which no variation is described. Where the species shows variability, the holotype has the following characteristics: snout from above with blunt point, loreal region vertical. Tibiotarsal articulation reaches posterior corner of eye; heels overlap when tibiofibulae are parallel to femora at right angles to body. Outer metatarsal tubercle present, distinguishable. Color pattern as shown in Figure 14, lateral brown streak broken into series of spots, no spots on belly. Measurements: (in millimeters) snout to vent: 35.2; snout to end of coccyx: 33.5; knee to knee: 28.4; tibiofibula: 15.7; head length: 9.2; head width: 8.6; eye diameter: 3.0; snout to eye: 4.6; interorbital distance: 3.2; width of eyelid: 2.2.

REMARKS.—The AMNH catalog shows the type locality as in Guayas Province, and notes made by Tate would indicate it is near the Guayas-Azuay border. Tate did not indicate what province he was in when he collected the type series, but he was on the mule trail from Naranjal to the highlands, and he estimated the altitude at the river to be about 1400 feet above Naranjal, or approximately 500 meters. He noted that it was three hours by trail from Naranjal to the river, which was at the foot of the "real hills." He found the area through which the river flows to be very wet, but from there on the area became much drier. Since the trail passes the 500-meter contour well before the Guayas-Azuay border is reached, I agree the specimens were probably collected in Guayas Province.

Rivero discussed the type series, and figured the specimen here designated as the holotype (1968:22; pl. 3: fig. 5). On the legend of the plate the AMNH catalog number is given as 17738 rather than 17638, which can be read on the photograph. Rivero considered the specimens possibly to be conspecific with *Atelopus longibrachius* Rivero, a Colombian species. When *A. balios* is compared with descriptions of the type material (Rivero, 1963:112; Cochran and Goin, 1970:135), the differences in color pattern are distinctive, as pointed out by Rivero,

and there are additional differences in the number and distribution of pustules, the length of the forelimb, the presence and size of tubercles on the palm and sole, and in other characters. Geographically the localities for the two taxa are widely separated. Much collecting has been done by many workers in the area between the two type localities, but nothing resembling either taxon has turned up in collections as yet.

In the same paper Rivero (1968:22) indicated that some of the AMNH specimens from the Río Pescado belonged to *Atelopus spurrelli* Boulenger, a Chocóan species. He has reference to AMNH 17548-49, which are marked differently, and the pattern is certainly reminiscent of that of *spurrelli*. I have noted, as well, that these two specimens have a somewhat more prominent snout tip, which is slightly hooked downward, as is seen in *A. longirostris*, and the third digit on the forefoot seems to be markedly longer than in the type series. The color pattern could be formed from fusion of the discrete spots seen in the type series, however, and this is what I think has happened, so I am regarding the specimens as members of the new taxon.

I do not regard them as typical, and they are not designated as paratypes.

ETYMOLOGY.—The specific name is derived from the Greek word *balios*, meaning "spotted" or "dappled," and refers to the dorsal pattern of the members of this taxon.

SPECIMENS EXAMINED.—ECUADOR: (Guayas Province; Río Pescado (AMNH 17619-30, 17636-38, USNM 193957-58). All are paratopotypes. Assigned to this species, but not designated paratypes: ECUADOR: Guayas Province; Río Pescado (AMNH 17548-49).

Atelopus bomolochos, new species

FIGURE 15

HOLOTYPE.—CAS 93910, female, from Ecuador, Azuay Province, Sevilla de Oro, approximately 2800 meters. Collected January 9, 1958, by G. Frymire, A. Embree, and S. Strobel.

DIAGNOSIS.—A member of the *ignescens* group, most similar to *ignescens*, from which it is distinguished by the light dorsal coloration often marked with irregular dark spots; ratio head length/stand-

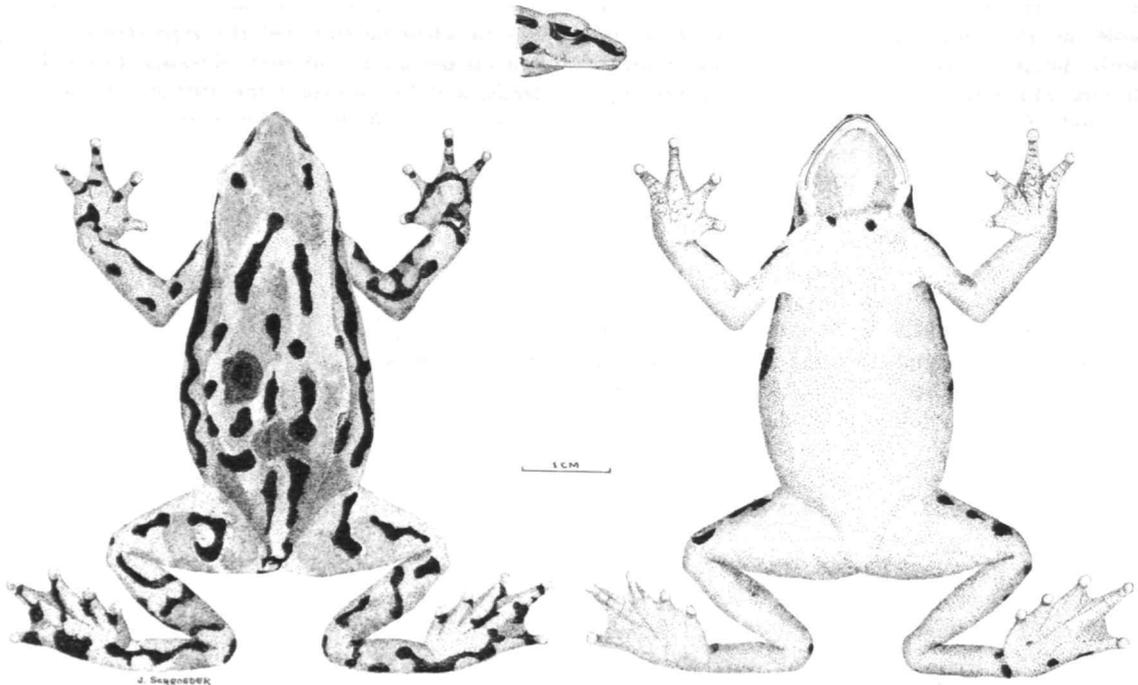


FIGURE 15.—Holotype, CAS 93910, of *A. bomolochos*, new species.

ard distance $\times 100$ usually greater than 33; warts and pustules absent on upper arm, crus, and ankle, but present on sides from tympanic area to groin, usually absent on dorsal and ventral surfaces of body; first digit on forefoot distinct, almost totally free of webbing.

DESCRIPTION.—Snout from above gently rounded or with blunt point; distinct angle above nostril; snout, canthus, and upper eyelid fleshy and raised, with flattened, glandular, fleshy ridge from posterior corner of eye to end of head. Dorsum of head between fleshy areas slightly concave or flat, smooth. Eyes protrude laterally, dorsal area of eye in same plane as rest of head. Snout from side extends short distance beyond level of lower jaw and upper lip, nostril lateral, occasionally directed slightly backward, on raised, rounded area. Loreal region distinctly concave; fleshy area over eye fused with upper eyelid; upper lip slightly fleshy. Temporal area studded with glandular prominences, rounded in males, covered with spiny points in females. Middorsum of body completely free of warts, glands, or pustules; usually quite smooth. Dorsolateral area of neck with heavy, glandular fold, shelflike in appearance, extending back from dorsolateral temporal fold, sides wrinkled and folded, covered by small white or yellow pustules from tympanic area to groin, and on upper arms and thighs; pustules may be single and evenly scattered or bunched together. Chin, chest, and belly with wrinkles and folds, most prominent on chest. No pustules or spicules on ventral surfaces, although occasional individuals show very tiny spiculations on chest.

Forelimb short and heavy; upper humeral region with spicules, but lower humeral region and forearm free of spicules, smooth or coarsely wrinkled. When forelimb is stretched along body, fingertips do not extend beyond posterior margin of thigh. Flesh of forefoot swollen; all digits free, with fleshy webbing only at base. Sole of forefoot covered with raised, rounded, glandular areas, subarticular tubercles not differentiated from these pustular areas; palmar tubercle larger and well defined. Males with horny excrescence on first and second digits, first usually strongly flexed, with prominent, thick, rounded fleshy hump dorsally, keratinized area wide and extending from tip of digit to its base; second digit with cornified area narrow, extending from base of digit to terminal articulation.

Hind limb short, stout; femoral region spinose on upper thigh only, close to body, rest of limb smooth or slightly wrinkled, occasionally with glandular areas on thigh and crus. Tibiotarsal articulation reaches to points at arm insertion when carried forward along body; heels are separated when tibiofibulae are parallel to femora at right angles to body. Foot fleshy, with very indistinct scattered pustules on sole; webbing fleshy, extends to digit tips as fringe except on first toe, which is almost completely hidden in webbing; webbing between all digits except first and second deeply incised. Outer metatarsal tubercle raised and prominent, inner metatarsal tubercle indistinct.

COLOR IN ALCOHOL.—Dorsum of head, body, and limbs light, may be yellowish, yellow-green, or light brown; occasionally uniform, but usually with few to many irregular, scattered, dark brown to black spots. Dark dorsolateral line begins on side of snout just below fleshy fold, runs through eye and across temporal region onto sides, where it may be continuous and broad, narrow and jagged, or almost totally absent. Ventral surfaces unicolor white, yellowish white or yellow; occasional individual with one or two small brown spots on throat or below anus. Spots often present at limb articulations, may extend around limb, but in no instance continuous ventrally. Sole of forefoot always unicolor, sole of hind foot usually unicolor, may be spotted or streaked.

HOLOTYPE.—This specimen conforms with the description given above for the species, where no alternatives are given. In the case of alternatives, it has the following characteristics: snout rounded; dorsum of head slightly concave, temporal region lightly pustulate. Skin on chest and throat lightly spiculate. Dorsum yellowish, with many black spots, dorsum of limbs with black reticulation; two black spots on throat at chest. Measurements of type (in millimeters): snout to vent: 50.4; snout to end of coccyx: 45.0; knee to knee: 34.6; tibiofibula: 17.0; head length: 12.7; head width: 12.6; eye diameter: 4.0; snout to eye: 5.7; interorbital distance: 3.8; width of eyelid: 3.6.

REMARKS.—The tendency seen in these individuals to have spots of color at the articulations of the limbs is reminiscent of the stronger development of rings around the joints in *A. boulengeri*. This species is comparatively large, and could cer-

tainly be considered as a close relative of *boulengeri*.

Of the seven species described as new in this paper, *bomolochos* is perhaps of most questionable validity. It is clearly closely related to *ignescens*, and, as is pointed out in the discussion of that species, the variability of *ignescens* is considerable. It could easily encompass the differences on which *bomolochos* is based, although I have as yet seen specimens with the particular constellation of characters used to define *bomolochos* only from a comparatively limited area. There is a distinct possibility that the two taxa are sympatric, although there seem to be no existent collections where a single series contains both taxa. Both the California Academy and the University of Kansas have had active collectors working along the Pan-American Highway in Cañar, Azuay, and Loja Provinces in the last few years, and a fairly continuous series of *ignescens* can be put together from the available material. While these southern specimens are not identical with northern populations, they are not so distinct that I think any purpose would be served by describing them as different. A single individual tentatively called *bomolochos*, CAS 93906, is from a locality well to the north of the remaining sample, and was also collected along the Pan-American Highway. There is a small series from Cuenca which I feel is legitimately associated with the new taxon. This locality, too, is on the highway. Specimens called *ignescens* in this paper come from both north and south of these two localities on the highway, and one gains a distinct impression of either interdigitation or sympatry.

The two taxa, *bomolochos* and *ignescens*, are not distinguishable on the basis of any of the measurements shown in the figures, with the possible exception of head width/head length. There are insufficient males of *bomolochos* available for statistical analysis, but the females of *bomolochos* are distinct from those of *ignescens* with regard to this character. Otherwise, the variation in *bomolochos* is almost completely within that expected or observed in *ignescens*.

It is worth noting that both workers from the University of Kansas and several of my field parties have collected in the area from which *bomolochos* is recorded without obtaining specimens. My party, including two students, an experienced Ecuadorian collector, and Dr. C. F. Walker, was

in Sevilla de Oro in July 1962, but we took no *Atelopus* at all. The *ignescens* material at the University of Kansas was collected in the months of May, June, and July. The California Academy collectors of the type material were in the area in the months of January and February. This seems to indicate a seasonal occurrence and disappearance for *bomolochos*, but may simply reflect the breaks of the game.

ETYMOLOGY.—The specific name is directly from the Greek word *bomolochos*, meaning "toady," or "lickspittle." While perhaps a stretch of the imagination for those who believe in strict interpretation of the literal meanings of words, it delights me to think of the species as a "toady type frog," or, for that matter, since it is a bufonid, a "toady type toad."

SPECIMENS EXAMINED.—The following are designated as paratypes: Azuay: Sevilla de Oro, 2800 m (CAS 85341-42, 93910; holotype: 93912, USNM 193956). The following are tentatively identified as *bomolochos*, but are not designated as paratypes: Azuay: Cuenca, 2535 m (CAS 85139-41, 85161). Cañar: between Juncal and General Morales, approximately 2500 m (CAS 93906).

Atelopus boulengeri Peracca

FIGURE 16

Atelopus Boulengeri Peracca, 1904:20 [type locality: "di Gualaquiza e parecchi di S. Jose, Ecuador orientale"].

Atelopus bicolor Noble, 1921:3, fig. 4 [type locality: Cordillera Kutuku, east of Macas, Ecuador, 1800-2000 m].—Rivero, 1963:107.

A.[telopus] boulengeri.—Nieden, 1926:82.—Rivero, 1963:107.

SYNTYPES.—Six specimens, UT An. 560, from San Jose, and eleven specimens, UT An. 559, from Gualaquiza, in the Zoological Museum of the University of Torino, Italy.

DESCRIPTION.—Snout from above with rounded tip, outward curve of muzzle becoming inward curve from nostril to eye; snout, canthus, and upper eyelid fleshy and raised, with fleshy ridge from posterior corner of eye to edge of head. Dorsum of head between these raised, fleshy areas flat, broad and smooth, lying in same plane as broad, flat back. Snout from side slightly protrusive beyond upper lip and lower jaw, nostril lateral, below fleshy area of canthus, and directed slightly posteriorly. Loreal region strongly concave behind nostril; eye over-

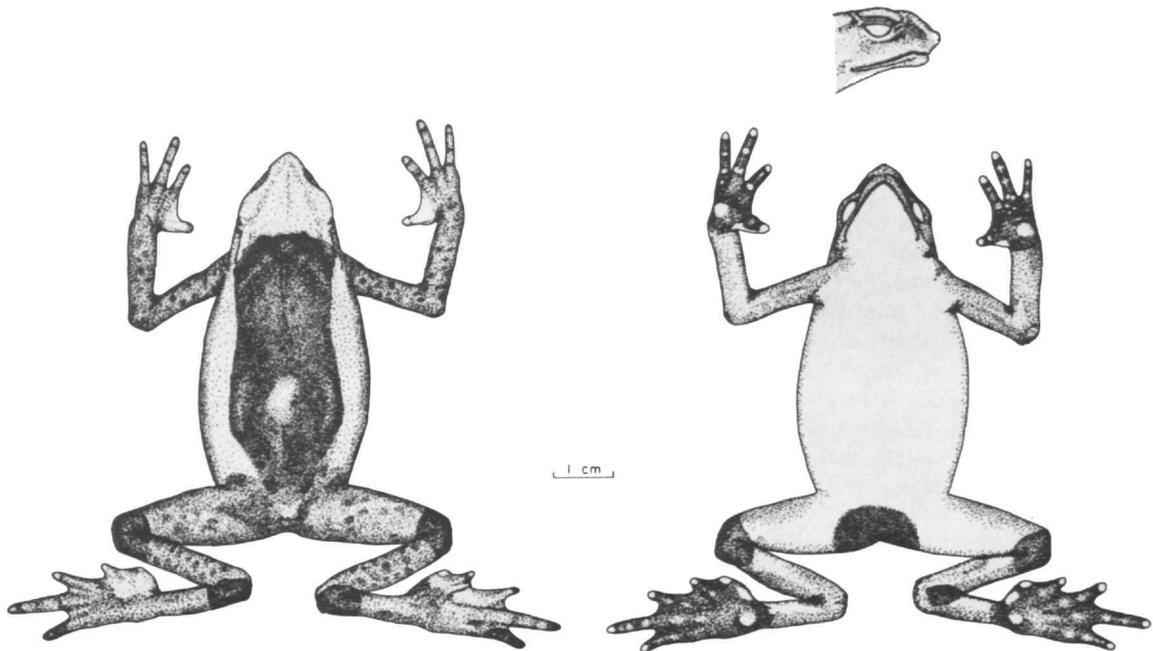


FIGURE 16.—A representative individual, USNM 193491, of *A. Boulengeri* Peracca.

hung by fleshy margin of eyelid, upper lip somewhat fleshy. No tubercles or pustules anywhere on head or body. Dorsum and sides of body smooth or finely wrinkled, belly with more prominent and distinct wrinkles.

Forelimb slender, forearm usually somewhat more fleshy than humeral region, dorsum weakly pustulate, rest of arm smooth. When forelimb is pulled back along body, palm of hand reaches vent. Entire hand fleshy, quite heavy around first digit, which is clearly distinct and prominent, second digit shorter than fourth, subarticular tubercles at base of digits only. Tips of digits prominent, slightly swollen ventrally. Palmar tubercle distinct, plantar tubercle present. Edge of prepollex with horny excrescence in males.

Hind limb slender, smooth except for few low, very indistinct pustules on dorsum. Tibiotarsal articulation reaches to points between posterior margin of eye and arm insertion when carried forward along body; heels do not overlap or touch when tibiofibulae are parallel to femora at right angles to body. Entire foot with fleshy webbing to tips of toes; webbing somewhat excised between

last three toes and reaching tip of fourth toe as fringe only; first and second toes almost totally hidden in webbing, tips of all toes free and somewhat prominent, with slight swelling. Subarticular tubercles weak, outer metatarsal tubercle raised and prominent but smaller than the flattened, rounded inner metatarsal tubercle.

COLOR IN ALCOHOL.—Dorsum usually unicolor, chocolate brown, dark brown, or blackish; extending slightly onto sides of body, where it is sharply set off by yellow of sides and belly, both of which are also unicolor. Dorsum of head with dorsal color extending to varying degrees anteriorly; in some it ends at eye level, in others it covers snout. Side of head, lips, chin, and throat all monochrome yellowish. Limbs usually slightly darker yellow than venter, with rings of brown around all joints. Dorsum of first finger and first two toes often lighter than rest of foot. Ventral surfaces of feet usually dark, with lighter tubercles. Brown of dorsum usually extends over posterior margin of legs and forms brown "seat" or "diaper" on rear of venter, with anus usually bright yellow in center of this brown area.

COLOR IN LIFE.—Rich chocolate brown dorsally, with bright yellow laterally and ventrally.

ECOLOGY.—The two specimens collected in 1962 were found along a trail in fairly heavy subtropical forest, in full daylight, about 11:00 A. M. Both were walking, not hopping, along the trail, fully exposed, and made no effort to avoid being captured.

SYNTYPES.—The 17 syntypes agree completely with the description above, with the series exhibiting all the variations mentioned in the description. Some of the specimens from Gualaquiza are somewhat dried, and the digits do not have either as thick or as full a webbing as in fresh specimens, but the San José series is in good condition, and the digits are as described. Only one specimen in the series shows a yellow area at the anus; the rest have the anal region the same color as the dorsum.

COMPARISONS.—The differences between *boulengeri* and *bicolor* appear to be the consequence of differences between investigators, rather than between the types. The primary distinguishing characters pointed out by Noble in the description of *bicolor* were the development of the webbing and several proportions. Noble said the digits of the forefoot were webless, while Peracca described the webbing between the second, third, and fourth fingers as rudimentary, and as relatively well developed between the first and second fingers. The area between these digits is actually quite fleshy, and it appears that Peracca considered this fleshiness equivalent to webbing, while Noble, who illustrated this area clearly in his figure, thought it should not be called webbed at all. The description of the webbing of the hind foot by Peracca is quite consistent with Noble's figure, although Peracca described the foot as strongly webbed, while Noble said, "toes webbed to the tips . . . but the web deeply indented, making the toes appear half webbed." The differences in proportions are quite minor, and could easily be the result of different techniques in measuring. Thus, in *boulengeri* the head length is contained in the body length $2\frac{1}{2}$ to 3 times, according to Peracca, while in *bicolor*, according to Noble, the body is $3\frac{1}{2}$ times as long as the head. But Noble clearly indicated that the head length meant from snout to angle of jaw, and no one knows for sure how Peracca made his head length measurement. There are several other stan-

dard head length measurements that might give a larger value, and thus a smaller proportion, for Noble's specimens.

Although there may have been some geographical validity for retaining the two species prior to our field work in 1962, the two specimens we obtained weaken this validity considerably. The type series for *boulengeri* came from Gualaquiza, a town in the valley of the Río Zamora, at 950 meters. Noble's specimens came from quite a bit higher in an isolated Cordillera to the east of the valley of the Río Upano, a tributary of the Namangoza, which joins the Zamora to form the Río Santiago. The two new specimens come from the eastern slopes of the main Andean chain at an altitude of 1560 meters, and some distance to the west of the valley of the Namangoza. This indicates an altitudinal range of about 600 meters, with the species occupying the foothills and mountain slopes of the headwater streams of the Santiago up to an altitude of 1560 meters.

Rivero (1963:110) regarded *A. bicolor* Noble as probably not referable to any other Ecuadorian species, but later (1968:23) indicated that it is "certainly a synonym of *A. boulengeri* Peracca." He records four specimens from Turula, which he indicates as being east of Macus, but there is only one specimen in the AMNH from Turula, which is a "tambo" on one of the mule trails from Riobamba to the Amazonian region, and lies northwest of Macas. The *bicolor* paratypes, AMNH 13133-35, are not from Turula (see below).

SPECIMENS EXAMINED.—ECUADOR: no additional data (AMNH 17427-28, 17430-31). Morona-Santiago Province; Cordillera Cutucú (AMNH 13132—holotype of *bicolor*, AMNH 13133-35—paratypes of *bicolor*, UKMNH 108940, USNM 193493), Gualaquiza (UT An. 559—syntypes of *boulengeri*), Río Piuntza, 1830 m (UKMNH 147071-81), San José (UT An. 560—syntypes of *boulengeri*), Turula (AMNH 33893), between Mirador and Copal, on mule trail from Sevilla de Oro to Mendez, 1600 m (USNM 193491-92). Loja Province; San Ramón (JAP 8934).

Atelopus bufoniformis Peracca

FIGURE 17

Atelopus bufoniformis Peracca, 1904:20 [type locality: El Pun, Ecuador].

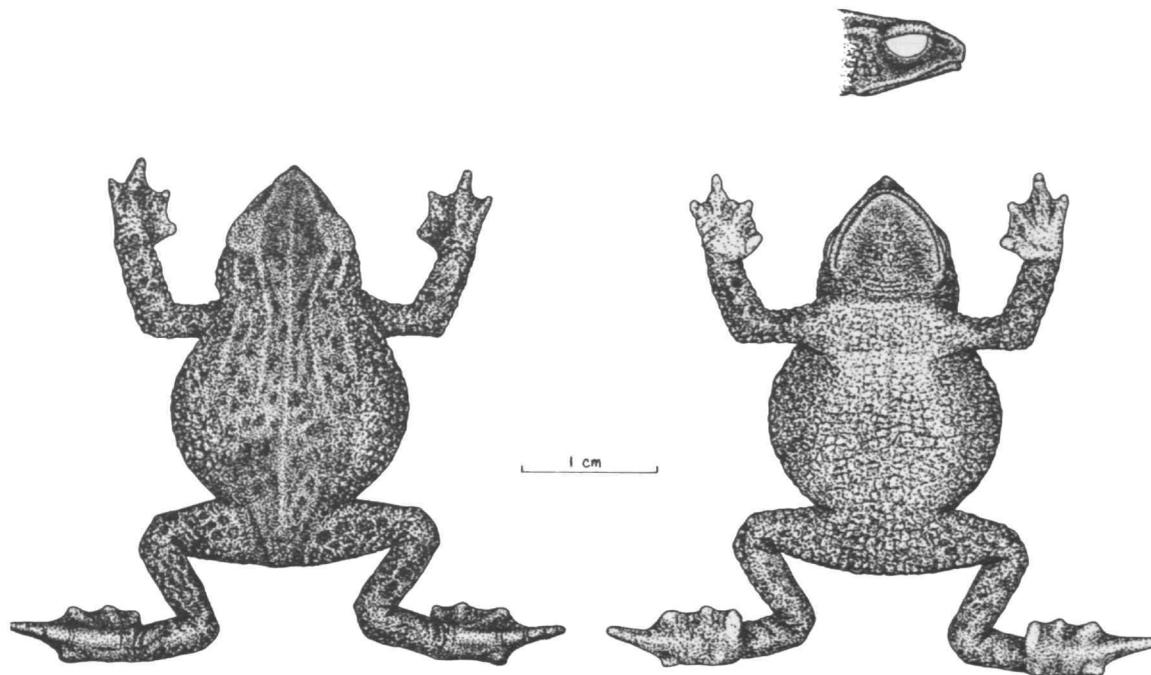


FIGURE 17.—A representative individual, USNM 193537, of *A. bufoniformis* Peracca.

SYNTYPES.—Two specimens, UT An. 561, in the Zoological Museum of the University of Torino, Italy.

DESCRIPTION.—Snout from above angulate and pointed, with a sharp angle at level of nostril; canthi from nostril to eye almost parallel, without a curve; eye strongly protruding and directed slightly forward; canthus fleshy and raised above median area of snout; dorsum of eye fleshy with many wrinkles and grooves. Dorsolateral area of head behind eye with a prominent ridge from eye level extending posteriorly along back, converging on ridge from opposite side to a point above shoulder, at which point they diverge until they disappear. Second, more glandular ridge arises at corner of eye and runs over tympanic region, either ending in small boss at end of head, or continuous with a glandular dorsolateral fold. Rest of head dorsally covered with wrinkles, grooves, and pustules. Snout from side extends very slightly beyond end of lower jaw, and is either bluntly rounded or weakly pointed. Loreal region vertical, not concave; entire side of head with rather thick skin, wrinkled, grooved, and with small, fleshy, flattened

warts, increasing in prominence over tympanic area. Entire body, limbs, chin, throat, and belly heavily pustulate or warty, with pustules low and flattened.

Forelimb very short, slender. When limb is carried along body, digits barely reach insertion of hind leg. Hand with very fleshy webbing enclosing first digit completely, second and fourth almost as completely, and on third digit to tip as fringe, with whole foot giving appearance of toad wearing a mitten. Entire lower surface of hand as heavily pustulate as rest of body, obscuring sub-articular tubercles completely; plantar tubercle very vaguely defined. Hind limb short, slender; tibiotarsal articulation reaches to points on side well behind axilla when leg is carried forward along body; heels widely separated when tibiofibulae are parallel to femora at right angles to body. Entire foot with very thick, fleshy webbing, enclosing fully all digits except fourth, which is fringed to tip by web. No distinguishable tubercles on sole, which is fleshy and wrinkled; outer metatarsal tubercle vaguely defined, inner metatarsal tubercle even more vaguely defined.

COLOR IN ALCOHOL.—Dorsum of body, head, and limbs entirely very dark brown to black; only occasional individuals with somewhat lighter brown vermiculations on back. Venter of body brown, with more or less vague dull yellowish mottling. Sole of feet lighter than rest of ventral surfaces.

COLOR IN LIFE.—USNM 193537 was very reddish in life, and the warty pustules on the venter were a very bright red. USNM 193538 had yellow pustules on the venter.

SYNTYPES.—The two syntypes are badly dried, but it is still possible to identify them as *bufoniformis* in the sense of this paper. The larger of the two syntypes is the individual for which measurements are presented in the original description. The second specimen is about 20 millimeters long. The larger specimen fits the description above except as follows: the glandular ridges arising at the corners of the eye are continuous with the glandular dorsolateral folds. The snout from the side is bluntly rounded. The specimen is too badly dried to carry foot forward, but Peracca said that the tibiotarsal articulation “raggiunge scarsamente la spalla.”

REMARKS.—This is a very small species. The largest individual seen measured 33 millimeters from snout to end of coccyx, and most specimens were less than 30 millimeters long. The shortened limbs and increased padding or fleshiness of the feet seem to be highly adaptive, providing reduced surfaces for heat loss. The species seem well adapted for high altitude life, and has been taken as high as 3700 meters.

Cochran and Goin (1970:120) described and figured a single specimen of this species from the Páramo de las Papas, Cauca, Colombia. It is correctly identified, and thus *A. bufoniformis* shows a wider distribution than any other highland species except *A. ignescens*. As I have pointed out elsewhere in this paper, these are the only two species that have been able to break out of the isolating mechanisms faced by all high altitude species of *Atelopus*, and extend their distribution into higher areas of both Ecuador and Colombia.

SPECIMENS EXAMINED.—ECUADOR: Napo Province; El Pun (UT An. 561-syntypes), Environs of Santa Barbara (USNM 193537–40). Carchi Province; Páramo del Angel, 23 km SW of Tulcan, 3700 m (UKMNH 117880). Imbabura Province: Cordillera de Intag, La Delicia, 2700 m (UKMNH

132126), N slope of Nudo de Mojanda, 3400 m (UKMNH 131797–98).

Atelopus elegans (Boulenger)

FIGURE 18

Phryniscus elegans Boulenger, 1882a:155 [type locality: Tanti, Ecuador, 2000 feet]; 1882b:464, fig. 1.

Atelopus elegans.—Boulenger, 1894:375; 1898:119.—Peracca, 1904:22.

A. [telopus] elegans.—Nieden, 1926:81.

Atelopus [elegans] elegans.—Rivero, 1963:109.

HOLOTYPE.—British Museum (Natural History), one female.

DESCRIPTION.—Snout from above rounded, not ending in point; distinct angle in canthus at nostril level; canthus and upper eyelid not fleshy, dorsum of head smooth and flat. Snout from side with distinct projection, ending in blunt point, extending beyond symphysis of lower jaw; loreal region vertical, not concave. Head dorsally and laterally smooth, without spines, warts, or pustules. Body slender, skin completely smooth.

Forelimb long, slender; when laid back along body, palm reaches anus. Webbing fleshy, enclosing and almost completely obscuring first digit; full webbing between first and second digits; web extends to tips of other digits but is deeply incised between them. Fourth digit extending beyond level of penultimate joint of third; considerably longer than second digit. Palm of hand fleshy, with deep folds; palmar tubercle low, rounded; plantar tubercle weak and indistinct.

Hind limb long, slender; when brought forward along body, tibiotarsal articulation reaches points between loreal region and posterior margin of eye; heels overlap when tibiofibulae are parallel to femora at right angles to body. Hind foot with thick, fleshy webbing; first and second digits almost totally enclosed, with only their tips distinguishable; other digits with full webbing that is shallowly incised, and extends to tip of fourth digit as fringe only. Fifth toe longer than third. Sole of foot quite fleshy with deep grooves or folds, no clearly defined subarticular tubercles; outer metatarsal tubercle poorly defined, inner metatarsal tubercle almost indistinguishable.

COLOR IN ALCOHOL.—Dorsal ground color white, with more or less regular pattern of brownish or

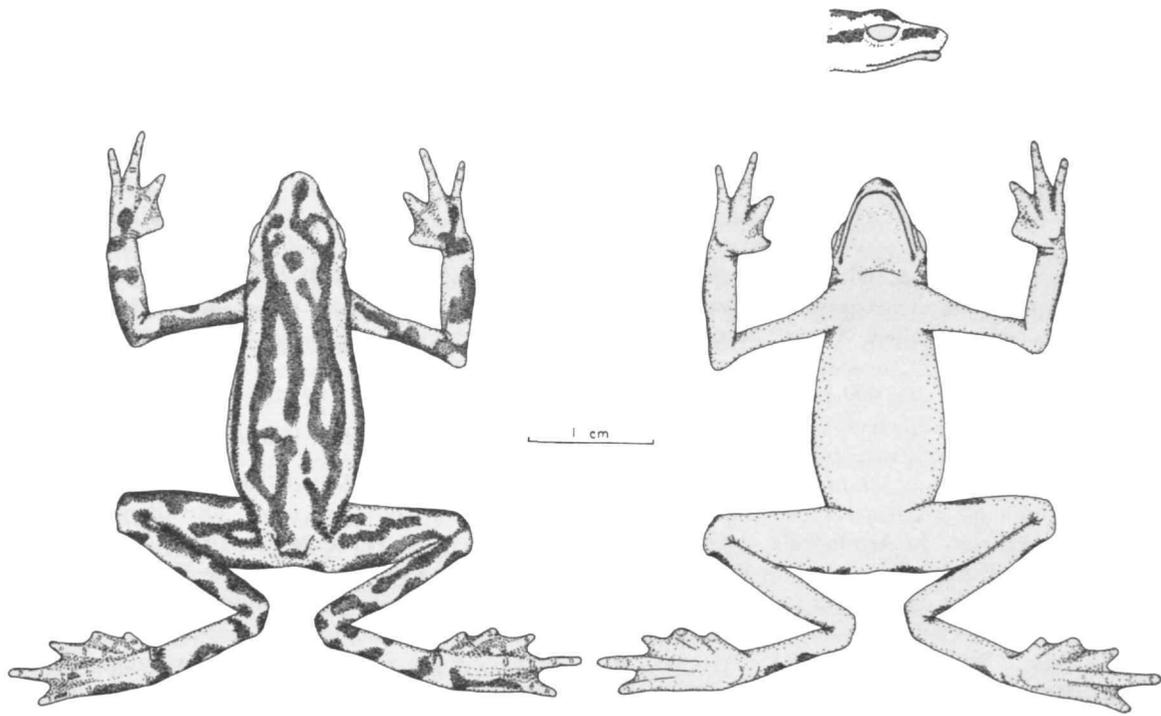


FIGURE 18.—A representative individual, UMMZ 51270, of *A. elegans* Boulenger.

black consisting of parallel stripes beginning on eyelid, where they may be joined by bar between eyes, and extending to just short of anus, which is usually in isolated spot of brown narrowly separated from stripes. Dorsal stripes irregularly connected by vermiculations and lateral bars, or separated by additional stripes running lengthwise, by light spots surrounded by brown borders, or by brown spots surrounded by white. Solid white line from eye to groin along dorsolateral line in most individuals, bordered below by dark line beginning at tip of snout, passing along lateral area of canthus, and continuous from eye to groin. No pigment on sides or belly below this lateral dark streak. Dorsal areas of limbs and feet mottled, streaked, and striped with dark brown to black, as body; ventral areas of appendages unicolor yellowish white.

COLOR IN LIFE.—Unknown, but several specimens are very yellowish in ground color, indicating that this might be the living color.

REMARKS.—Rivero (1963:109) regarded *Atelopus gracilis* Barbour, from Gorgona Island, Colombia, as a subspecies of *Atelopus elegans*. Cochran and Goin (1970:133) made *elegans* a subspecies of *A. varius*, with *gracilis* a strict synonym. They did not refer to Rivero's action in their synonym. Neither Rivero nor Cochran and Goin presented any documentation for the changes they made. Rivero stated that specimens from Ecuador "seem sufficiently distinct from Gorgonian material to make the island form deserve the racial name *A. elegans gracilis*." He does not describe the differences or define the race. Cochran and Goin reduced several species to the subspecific level within *A. varius*, but again the reasons for doing so were not clearly stated. Even though it is entirely possible that *elegans* represents the southern end of a genetic continuum which embraces both high and low altitude populations, I have seen no evidence to support the concept. *A. elegans* is a distinct, easily recognized, well marked taxon, and I prefer to

recognize it as a full species until intergradation with the subspecies of *varius* can be demonstrated. The relationship between *gracilis* and *elegans* may be subspecific, but I have not examined the *gracilis* material, and leave that question in abeyance for other investigators.

In 1955, I referred to the locality called "Bulún" in the American Museum catalogs as unlocated. Levi-Castillo, in an editorial footnote to my remarks, suggested that it was in reference to "Bulu-Bulu," a river in Guayas and Cañar Provinces. The United States Board on Geographical Names (1957, p. 138) lists a place called "Pulún" at the coordinates 1°05'N, 78°40'W, and it is shown at those coordinates on the 1:1000000 map of the Instituto Geografico Militar del Ecuador (1950). The American Museum specimens were collected at about the same time as material from Salidero and Río Durango, both of which are shown on a map of Esmeraldas Province in Acosta-Solís (1944, opp. p. 574). Both localities are very close to Pulún, which also appears on the map in the work by Acosta-Solís. The coordinates for Salidero would be approximately 1°04'N, 78°38'W, and the town lies on the Río Bogotá. The Río Durango enters the

Bogotá from the east about halfway between Salidero and Pulún. I am, therefore, using the name "Pulún" for the place where the AMNH specimens were collected.

SPECIMENS EXAMINED.—ECUADOR: Esmeraldas Province; Pulún (AMNH 10581–84, UMMZ 51270), Quinindé (USNM 193534), Río Cupa (UKMNH 108941, USNM 193535), Río Durango (AMNH 10585–88), Salidero (AMNH 10577, 10579–80, MCZ 2615, 7605). Imbabura Province; Lita, Río Mira (USNM 193536).

Atelopus halihelos, new species

FIGURE 19

Atelopus [species].—Rivero, 1968:21.

HOLOTYPE.—AMNH 16716, male, from Ecuador, Morona-Santiago Province, Cordillera Cutucú, collected by E. Feyer, March 1921.

DIAGNOSIS.—A member of the *ignescens* group, although limbs are more slender than other species; most similar to *nepiozomus*, from which it differs in having an almost indistinct first digit on the forefoot and in coloration, particularly in the

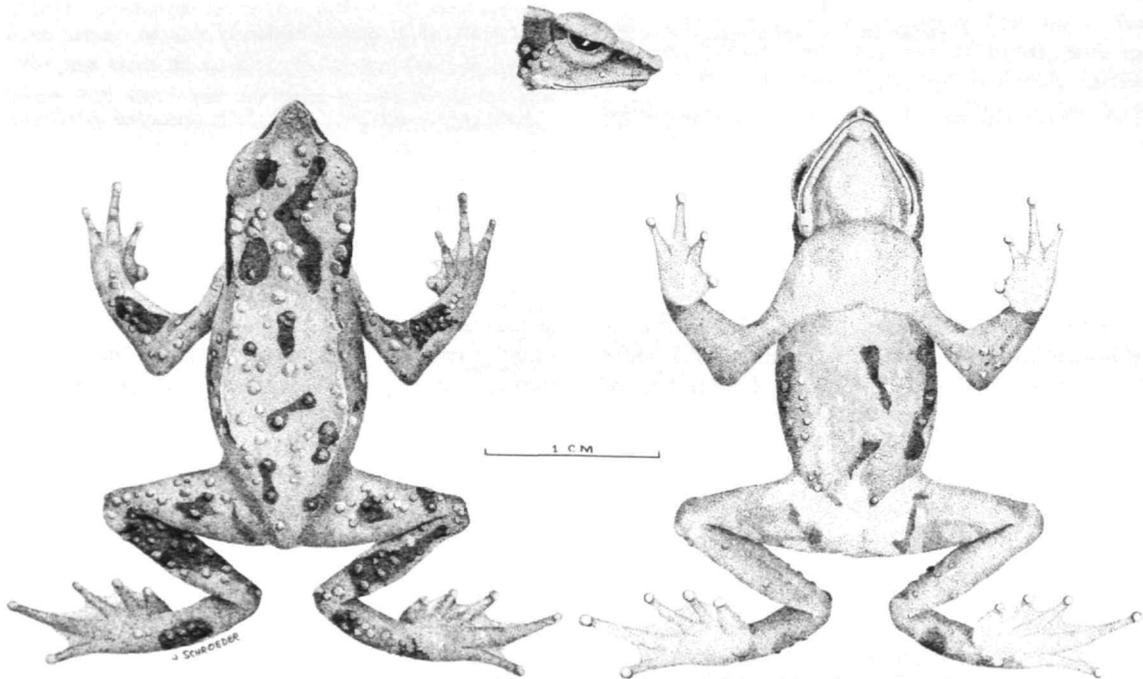


FIGURE 19.—Holotype, AMNH 16716, of *A. halihelos*, new species.

presence of a light whitish patch below the anus, in contrast to the dark "diaper" of *nepiozomus*.

DESCRIPTION.—Snout from above with rounded point, distinct angle in canthus rostralis at nostril; snout, canthus, and eyelid fleshy and raised, with either fleshy ridge or row of raised pustules from corner of eye along dorsolateral margin of head. Dorsum of head flat, with scattered, low, glandular pustules. Snout from side protrusive, pointed, extending well beyond upper lip and lower jaw; nostril lateral, below fleshy area of canthus, at top of rounded prominence. Loreal region flat or slightly concave; eye overhung by flap formed of fleshy area, flap has free edge and can be lifted away from the eyelid; upper lip swollen. Temporal region with low, glandular pustules, which may bear pointed spicules in either sex. Dorsum and sides of body smooth, with many low, rounded, scattered warts. Ventral surfaces may be either comparatively smooth or with flattened, indistinct glandular patches separated by wrinkles and folds.

Forelimb slender in females, shorter and more muscular in males, particularly in the forearm. When limb is carried along body, digit tips reach beyond posterior margin of thigh. Dorsal and lateral surfaces of limb covered with warts, more prominent in males than in females. Hand with fleshy webbing, first digit almost entirely enclosed, other digits free. Males with keratinized pad on dorsum of first digit, no horny excrescences on second digit. Sole of forefoot smooth or with few low pustules; plantar tubercle weak, defined by absence of pigment in area.

Hind limb long, slender, covered dorsally and laterally with low warts; tibiotarsal articulation reaches to area between eye and end of head when leg is carried forward along body; heels touch or are barely separated when tibiofibulae are parallel to femora at right angles to body. Webbing thick but not heavily fleshy, extending to tips of all but fourth digit, incised between all digits except first and second; only tip of first digit free of web. Sole almost entirely smooth, subarticular tubercles usually present, but low and often indistinct; outer metatarsal tubercle fairly prominent, distinct; inner metatarsal tubercle larger than outer, but low and indistinct.

COLOR IN ALCOHOL.—Entire body and limbs light brown, with small, scattered, irregular dark brown or blackish spots on all surfaces. Ventral area of

thighs and belly immediately below anus very light colored, often whitish, without spots.

HOLOTYPE.—This specimen conforms with the description given above for the species in those characteristics for which no variation is mentioned. In the case of variable characters, it has them as follows: a row of raised pustules along dorsolateral margin of head behind eye; loreal region slightly concave. Warts in temporal region do not bear spicules. Chest and throat with low, indistinct pustules. Heel carried forward along body reaches temporal region; heels do not touch when tibiofibulae are parallel to femora. Soles of both fore and hind foot with few indistinct tubercles, subarticular tubercles on hind foot slightly more prominent. Measurements of type (in millimeters): snout to vent: 25.3; snout to end of coccyx: 23.4; knee to knee: 20.3; tibiofibula: 9.8; head length: 7.8; head width: 7.2; eye diameter: 2.6; snout to eye: 4.0; interorbital distance: 2.6; width of eyelid: 2.2.

REMARKS.—This series of specimens was discussed by Rivero (1968:21), and he felt their affinity was closest with *A. bufoniformis*. Since there are neither enough females of *A. halihelos* nor males of *A. bufoniformis* available for statistical analysis, the two species cannot be directly compared on the graphs provided earlier in this paper. Relative position with regard to other species, however, shows that *halihelos* is more slender, with longer limbs, and it appears more closely related to *A. nepiozomus* and other species on the lower Amazonian slope than to the highly specialized, high altitude *A. bufoniformis*. As in the latter species, it appears that *halihelos* is a diminutive species, with the largest specimen in the type series less than 32 millimeters long.

There is no way to be sure about the actual distribution or altitudinal relationships of this new species. The Cordillera de Cutucú is a fairly isolated mountain mass to the east of the valley of the Ríos Upano and Namangoza, with the foot of the Cordilleras at approximately 1000 meters, and the highest point somewhat more than 2000 meters. I would predict that the species will be found at altitudes above the lower edge of the Cordillera, and possibly to the highest points. It seems to be a situation similar to that of *A. planispinus*, which inhabits the slopes of a similar isolated mountain mass to the north.

ETYMOLOGY.—The specific name is derived from the Greek *hales* or *halis*, meaning "in abundance, in heaps, crowds or swarms," and *helos*, a "wart" or "callus." The reference is to the large number of glandular swellings on the body and limbs of individuals of this taxon.

SPECIMENS EXAMINED (in addition to holotype).—The following are paratopotypes: ECUADOR: Morona-Santiago Province; Cordillera Cutucú (AMNH 16717–24, USNM 193959).

Atelopus ignescens (Cornalia)

FIGURE 20

- Phryniscus ignescens* Cornalia, 1849:316 [type locality: "in locis humidus circa Latacunga prope Quito," Ecuador].
Phryniscus laevis Günther, 1858:43, pl. 3: fig. A [type locality: "Panama. Quito. Chili"]; 1859:417.—Boulenger, 1882:151.
Phrynidium laeve.—Cope, 1867:196.
Atelopus laevis.—Cope, 1868:117.—Orton, 1871:693.
Atelopus ignescens.—Espada, 1875:139, pl. 1: figs. 7–9.—Boulenger, 1880:46; 1898:119.—Werner, 1901:600.—Peracca, 1904:19.—Parker, 1934:268; 1938:440.—Rivero, 1963:109; 1969:142.
Phryniscus laevis exigua Boettger, 1892:22 [type locality: "Zurucuchu, W-Andes of Cuenca, 3250 m, Ecuador"].
A.[telopus] ignescens.—Nieden, 1926:83.

Atelopus carinatus Andersson, 1945:15, fig. 5 [type locality: "Eastern Ecuador"].—Rivero, 1969:142, fig. 2.

Atelopus ignescens ignescens.—Rivero, 1965:137.—Duellman and Lynch, 1969:236.

HOLOTYPE.—In the "Museo Mediolanense," present state unknown.

DESCRIPTION.—Snout from above not prominent or projecting, gently rounded, with little or no difference in angle between tip of snout and eye; snout, canthus, and upper eyelid heavily fleshy and raised, with a glandular, fleshy ridge from posterior corner of eye to corner of head. Dorsum of head between fleshy areas flat, smooth, or very finely wrinkled. Snout from side only slightly protrusive beyond lip and lower jaw, nostril lateral and below fleshy area of canthus. Loreal region vertical or slightly concave; eye overhung by heavily fleshy upper eyelid, upper lip not fleshy. Temporal area studded with pointed tubercles in females, or with fleshy, glandular bumps in males. Middorsum of body completely free of warts, glands, pustules; either smooth or finely wrinkled. Dorsolateral area and sides of body in females heavily studded with rounded glands that have one to several raised, pointed spicules on them, giving spiny appearance; same area in males covered with low, rounded

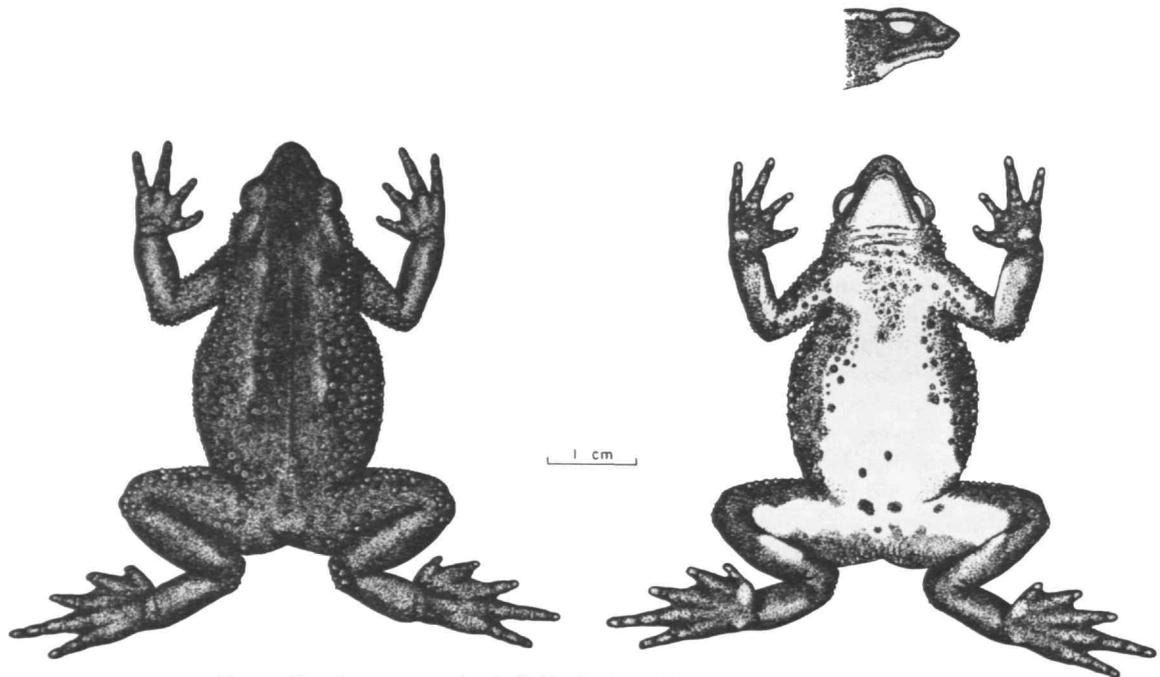


FIGURE 20.—A representative individual, JAP 4176, of *A. ignescens* Cornalia.

glandular areas without spicules. Chin and belly finely wrinkled and occasionally lightly shagreened on chest in males, same in females, but with tendency in some individuals to have darkened spiny area across chest.

Forelimb short, stubby, and fleshy; humeral region heavily studded with spicules in females, covered by small rounded glands in males; forearm in both sexes heavily fleshy but quite smooth, contrasting strongly with upper arm. When forelimb is pulled back along body, tips of digits do not reach past hind leg in males or past groin in females. Entire forefoot fleshy, all digits free and prominent, with fleshy webbing only at base. Sole of foot covered with pustules, subarticular tubercles not differentiated from these pustules, palmar tubercle larger and clearly defined. Males have horny excrescences on both first and second digits; first digit usually strongly bent under and flexed, with prominent thick, rounded, fleshy hump dorsally, keratinized area extends from tip of digit to base; second digit with cornified area only at base.

Hind limb short, stout, fleshy; femoral region studded with spines in females, heavily pustulate in males, crural area smooth and fleshy. Tibiotarsal articulation reaches to level of arm insertion when carried forward along body; heels are well separated when tibiofibulae are parallel to femora at right angles to body. Foot fleshy with many pustules on sole, webbing fleshy, extends to tips of digits as fringe except on first toe, which is almost completely hidden within webbing; webbing between all digits, including first and second, deeply incised. Subarticular tubercles not clearly distinguishable from pustules, outer metatarsal tubercle small but raised and prominent, inner metatarsal tubercle larger but not as raised.

COLOR IN ALCOHOL.—Dorsum of head, body, and limbs uniform black, extending down sides and ending abruptly at edge of belly, which is yellow to yellowish white. Some individuals have spotting on chest. Ventral surfaces below anus and on limbs often light brown to black; pigment distribution ventrally differs considerably from one individual to the next. Lower lip usually dark, same color as upper lip, and sharply distinct from rest of chin.

COLOR IN LIFE (from a series of 25 individuals collected near Quito June 6, 1959).—Dorsum dark brown to black, lightening slightly on dorsum of limbs. Dorsal color sharply set off from ventral

color along a line running from corner of mouth along the lateroventral line. Ventral surfaces highly variable, from a light cream unicolor to light cream with yellowish or orange border to unicolor yellowish to unicolor orange. The eye is a deep black, no pupil color can be distinguished. Often with a bright orange or yellow spot on ventral side of crus, and some have same on dorsum of foot. In this same series of 25, the following variation in color of the ventral surfaces was noted (individuals can occur in more than one tabulation): venter mostly dull orange-5; cream with orange in axilla and inguinal region-4; yellowish, with brightest yellow in limb insertions-2; yellow spot on dorsum of foot-6; yellow spot on ventral surface of crus-8; yellow venter with reddish orange in limb insertions-2; unicolor yellow-2; venter of limbs maculated with bright orange-1. A series from 5 kilometers west of Papallacta all had bright, tomato-red bellies in life but of course, now are identical with other alcoholics in belly color.

REMARKS.—Tadpoles presumably of this species have been described by Duellman and Lynch (1969:236). The material was taken at 3620 meters on the slopes of Cotopaxi Volcano. The tadpoles have a large suctorial disc behind the mouth which is used to anchor the individual to the underside of stones in swiftly flowing water.

It will be noted that I have continued the synonym of *A. carinatus* Andersson with *A. ignescens*. Rivero (1969:142) has recently reexamined the holotype of Andersson's species, the only known specimen, and thought that the species should be considered valid on the basis of several characters, including the "nuchal tank" formed by the protruding posterior margin of the frontoparietal and the raised edges of the suprascapulae, the shape of the snout, and the size of the eye. The first of these, I am convinced, is the result of the way the specimen was preserved. The others are extremely difficult to evaluate or quantify, seem of minimal value taxonomically, and are, to my eye, at least, occasionally duplicated in large series of *ignescens* from a single locality. It should also be pointed out that the type locality, vague though it is, is an area of intensive activity by herpetological collectors, and no additional specimens resembling *A. carinatus* has ever been obtained in eastern Ecuador, while hundreds of animals looking very much like the type continue to be collected in the inter-

Andean valleys. Until added material from the supposed type locality is available, I shall continue to regard this weakly defined form as a synonym of *A. ignescens*.

ECOLOGY.—*A. ignescens* is adapted to the most rigorous climates found in Ecuador where amphibians occur. It inhabits the high inter-Andean valleys, and has sufficient eurytopic abilities that it has crossed the inter-Andean *nudos* to invade neighboring valleys. It has also moved up the slopes of the highest mountains above tree line, where it is found in the cold, windy, and dry páramos. It is tolerant of temperatures well below levels at which other species of *Atelopus* become inactive, except perhaps *A. bufoniformis*.

The species engages in mass migrations, apparently at the beginning of the breeding season, and can be seen in the hundreds at such a time. I have seen two such migrations, the first of which was moving across the Pan-American Highway north of Latacunga on December 31, 1958. Large numbers of individuals were smashed on the road over a distance of four or five miles. All living individuals were crossing the highway in the same direction. Some mated pairs were seen.

The second such migration was seen in the páramos on the road from Quevedo to Latacunga, on January 22, 1959, at an altitude of 3600 meters. In this case, the movement was again in a single direction, and definitely downhill. A light drizzly rain was falling, and sufficient rain had already fallen to make the road somewhat treacherous, with standing puddles. In both cases, the migration seems to be toward standing water, presumably the place of egg deposition, but this was not verified by direct observation.

COURTSHIP AND MATING BEHAVIOR.—The migration seen in the páramos included many clasped pairs as well as males ready to clasp. The males, always smaller than the females, clasp with an axillary grip. I followed one such pair for almost two hours, hoping to see egg deposition, but the female simply wandered about in what appeared to be a random way, never pausing anywhere long enough for any action to take place. The rate of progress is a slow, deliberate walk, never a hop or a jump. At one time the female entered a small puddle about five feet across and at most a foot deep, but she never broke either her stride or her pace, continuing to walk very deliberately across

the bottom of the puddle and out the other side. Experiments performed later with mated pairs in the compound of Robin Copping's house in Quito demonstrated that once the male has mounted the female he will remain in place no matter what the female does until the eggs are deposited. This may be a matter of several weeks, during which time the female feeds and moves about normally, but the male does not feed while he waits. The period of waiting for the male may not be so long under normal conditions, of course, but I suspect it is usually much longer than in other frogs.

The activity period is diurnal, and I have never seen members of this species active at night. The males seek out the females entirely visually. While they do make a slight sound, it is a very low, chick-like peep, difficult to hear even at short distances, and made while walking about looking for a female, rather than made in a stationary position to which a female could be attracted by the "call." As they walk about they will occasionally pause, raise themselves high on the forelimbs, and look about, scanning the horizon for other members of their species. There is no sexual discrimination in this scanning, because the individual moves off in the direction of another frog as soon as the second is seen, and attempts to mount. If the second is a male, the first is repelled by slow kicking and soft peeping. If the second is a female, it can usually be successfully mounted. If the second is a female with another male already in mounted position, the approaching animal is not put off for a second by the fact of prior possession. He will, if permitted to do so, mount the first male, and clasp him. Almost invariably, however, he is repelled by the first male. Since all the movements by this species are slow and deliberate, the repulsion almost appears to be in slow motion, but it still is effective. The mounted male raises his hind foot on the side of the approaching male, puts it very deliberately in the face of the intruder, and softly but forcefully kicks him away. The intruder usually describes a gentle arc, landing on his back, and the mated pair moves away as he slowly struggles to turn over. If they have not gone far enough by the time he recovers his equilibrium, a second attempt will be made and the same sequence enacted.

SPECIMENS EXAMINED.—I have seen over 500 individuals of this species, from all of the inter-

Andean valleys of Ecuador, from Tulcán south to the region of southern Cuenca Province. It seems of little value to list them in detail until someone has examined them more carefully for infraspecific variation.

Atelopus longirostris Cope

FIGURE 21

Atelopus longirostris Cope, 1868:116 [type locality: "Valley of Quito," Ecuador].—Orton, 1871:693.—Espada, 1875:155.—Nieden, 1926:81.—Guibe, 1948:32.

Atelopus varius [not Stannius].—Boulenger, 1880:46.

Phryniscus longirostris.—Boulenger, 1882:153.

Phryniscus boussingaultii Thominot, 1889:28 [type locality: "Entre Latacunga et Guayaquil, au sud de Quito," Ecuador].

HOLOTYPE.—Apparently lost. Not located in either the Academy of Natural Sciences of Philadelphia or the National Museum of Natural History.

DESCRIPTION.—Snout from above strongly projecting, with comparatively sharp point, distinct inward curve from snout tip to nostril, canthi

almost parallel from nostril to point just before corner of eye where each canthus flares outward; area from snout tip along canthus, outer eyelid border, and to corner of head raised and fleshy. Dorsum of head flat, shagreened; eyes prominent, protrusive. Snout from side strongly protrusive beyond lower jaw, with upper lip distinct from protrusion as well; nostril lateral, posteriorly directed, slightly below fleshy canthus, and almost directly above end of lower lip. Loreal region sunken, eye overhung by fleshy eyelid margin; vertical ridge behind eye and horizontal ridge from eye to corner of head; side of head and tympanic region shagreened, with few larger, white-topped pustules. Dorsum and sides of body heavily shagreened, with scattered white-topped pustules on sides only, belly almost smooth or with finely wrinkled surface. Vertebral column forms distinct, raised middorsal ridge from shoulder level to coccyx.

Forelimb very slender, forearm more fleshy than humeral region, pustulate on shoulder and dorsum of humeral region, shagreened elsewhere. Entire hand somewhat fleshy, heaviest around first

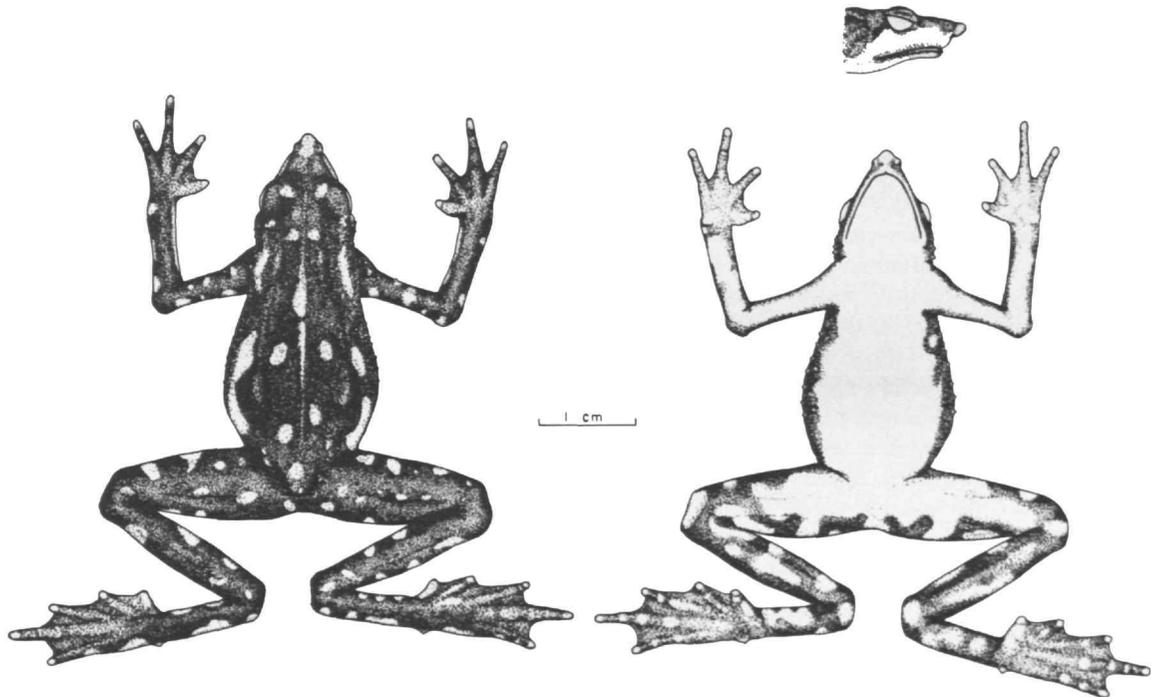


FIGURE 21.—A representative individual, USNM 193834, of *A. longirostris* Cope.

digit, which is distinct although almost totally enmeshed in fleshy webbing. Tips of digits slightly swollen; second digit shorter than fourth; second, third, and fourth digits almost free of webbing. Subarticular tubercles present only at digit base, weakly developed; large palmar, small plantar tubercle.

Hind limb long, slender, shagreened but without pustules; tibiotarsal articulation reaches points between nostril and posterior corner of eye when carried forward along body; heels overlap or touch when tibiofibulae are parallel to femora held at right angles to body. Fleshy webbing of foot extends to swollen tips of digits, but is incised between digits; first digit completely hidden in webbing, tip of second distinct. Subarticular tubercles present but weak; outer metatarsal tubercle raised, prominent; inner metatarsal tubercle elongate, flattened, kidney shaped.

COLOR IN ALCOHOL.—Dorsum brown, from reddish brown to very dark brown, snout tip light brown, sharply distinct from top of head, which usually has few scattered white spots, characteristically one on back of each eyelid. Dorsum with scattered, often bilaterally paired light spots; dorsolateral area over shoulder usually with elongate white spot, almost forming stripe in some individuals, usually followed dorsolaterally by one or two additional elongated spots or streaks. Sides usually unicolor, occasionally lightly vermiculated, abruptly changing into very light, immaculate yellow of belly, from chin to anus, with occasional individual showing brown vermiculations ventrally. Legs as body, usually unicolor brown above, spots laterally and dorsolaterally, light yellow below, posterior surface of thigh usually vermiculated. Tips of digits yellow, soles of feet usually dark, but some with yellow areas.

COLOR IN LIFE.—Dorsum blackish brown, shading into a light chocolate brown low on sides. Spots on head, back, sides, and dorsum of legs dull yellow. Those on back of femur white. Tip of snout yellowish brown, brighter than rest of spots. Series of tiny white stipples along sides and between eye and arm, behind temple. Eye black all over. Belly white, not flesh colored. Tips of digits very light orange. Stripe along upper lip yellow as dorsal spots, but grades into white of belly near corner of mouth. In a female heavy with eggs, the

eggs show brightly through the belly flesh, giving a strong orange tint to ventral surfaces.

ECOLOGY.—I have collected this species in several places on the western slope, and always found the specimens in rocky areas on the edges of streams. I have found individuals under rocks and also out walking about in and over the rocks in full sunlight. The habitat is not usually a shaded one, but is very exposed. A pair in amplexus was taken at Apuela on April 17, 1959, which was at the end of the rainy season. The female was heavy with eggs.

COMPARISONS.—An obviously close relative of *longirostris* is *A. varius glyphus*, described by Dunn (1931). The type and paratype series are in the National Museum of Natural History, and I have compared them directly with the series of *longirostris* available from Ecuador. In addition to the general similarity in color pattern, both species have rather slender bodies, elongate, thin limbs, and a comparatively prominent, overhanging snout. It is possible that the relationships of *glyphus* are not with *varius* at all, and it should be regarded as a distinct species. The two paratypes from Porto Obaldia, noted as quite different by Dunn (1931:396), are very reminiscent of *A. varius loomisi* Taylor (1952).

I have examined the holotype of *Phryniscus boussingaulti* Thominot, and see no reason not to continue its synonymy with *longirostris*. The specimen is badly faded dorsally, retaining no trace of pattern. There is a series of clear, rounded, whitish spots laterally, which, although not typical of *longirostris*, is almost duplicated in some of my specimens (e.g., USNM 193833). Photographs of the holotype were taken and are on deposit at the National Museum of Natural History.

REMARKS.—The type locality of this species, given as the "Valley of Quito" by Cope, is open to the same question as for the other four species described from the same place and collected by the Orton Expedition. Although one of these species (*Leimadophis alticolus*) has been found since in the immediate environs of Quito, the other three (*Bufo andianus*, *Dryadophis pulchriceps*, and *Dipsas oreas*) are clearly western slope species, usually at altitudes well below that of Quito. The road to Nanegal, on the western slope, is an easy one to travel, and a three-hour drive today puts one into the range of all of the species. I believe

that a local collector brought into Quito the material that eventually served as the types of these species for Cope, just as today several local collectors still find valuable and interesting material around Mindo, Tandayapa, and Nanegal.

This problem is complicated by the fact that Orton (1871) indicated that the type came from Hacienda Antisana, which he said was at an altitude of 13,300 feet. This locality, according to Cope (1868:96) is on the western slope of Volcán Antisana. Cope indicated that the total collection at this locality was "a small black frog," a description more appropriate to *A. ignescens* than *longirostris*. I think we can safely assume that Orton was depending upon his memory when he indicated the type locality, and in this case it was faulty. It is of additional interest to note that the USNM catalogs do not include any records of specimens from Antisana collected by Orton, so it appears that the "small black frog" from there was deemed too insignificant to catalog.

A series of specimens collected by P. Hershkovitz in 1935 at Carolina, Imbabura Province, at 900 meters, is tentatively assigned to this taxon. In general appearance and morphology they closely resemble *longirostris*, but they are all quite small. The difficulty in calling them *longirostris* is caused by their color pattern. They are quite similar to each other, in the occurrence of many more rounded and more closely approximated yellow spots dorsally than is typical of *longirostris*, and the large, elongate spot immediately behind the head dorsolaterally, so characteristic of *longirostris*, is absent in all four specimens, as is the lighter coloration of the projecting snout. There is a more or less distinct, continuous yellow dorsolateral line on the specimens, while in *longirostris* the same area is occupied by a discontinuous series of spots. The specimens are the northernmost record for the species as I define it, and may show incipient divergence from the parent taxon. The possibility that the specimens represented the taxon called *Atelopus longirostris marmorata* by Werner occurred to me, but the dorsal pattern cannot be called "marmorate," in my opinion, although it is closer to that than are typical *longirostris*, and I have considered Werner's taxon unidentifiable (see elsewhere, under *incertae sedis*).

The large series of specimens available from Ecuador provides a sufficient basis to demonstrate

that Rivero (1963:112) was correct when he indicated that the Colombian specimens he tentatively assigned to *longirostris* (CNHM 43850-51) probably would not prove to be conspecific with that species. Part of his doubt came from the difference in known altitudes for Quito and Cisneros, in Colombia, but I have shown above that Quito is not a valid locality for *longirostris*. The series of specimens from Santander called *longirostris* by Cochran and Goin (1970:143) unequivocally do not belong to that taxon. Therefore, *longirostris* is not known from Colombia at the present time, but is confined to the lower western slopes of the Andes in Ecuador.

A series of specimens in the American Museum (AMNH 49943-46, 49948-50) are recorded as having been collected at "Mera, Río Pastaza," which is a town on the principal road descending from the high Andes to lowland Amazonia. This is such a zoogeographic unlikelihood that I challenge the validity of the original data rather than record the occurrence of the species on the Amazonian slope. The records show that the specimens were purchased from a professional collector, and the history of Ecuadorian herpetology is replete with erroneous records based on such purchased material. The specimens are in my opinion clearly members of the species *longirostris*, and I am sure that they came from the lower western slopes of the Andes in Ecuador. In addition to the fact that the locality does not make zoogeographic sense, it should be pointed out that collectors have been delivering specimens to European, United States, and Latin American collections from the Mera region for over 200 years, since it lies on one of the main trails to the east, but there are no records of other specimens of this species from the area. I do not include this locality as part of the known range of the species until verification of its occurrence there by further collections has been made.

SPECIMENS EXAMINED.—ECUADOR (PM 207, holotype of *boussingaulti*): Esmeraldas Province; Alto Tambo (USNM 193853), Carondelet (USNM 193847-48). Imbabura Province; Apuela (USNM 193819-21, 193823); near Peñaherrera (UMMZ 83662-66). Pichincha Province; Chontapamba (MCZ 84203-04, USNM 193834, 193854-64), Llambo, on road to Gualea (BMNH 1972.737, USNM 193824-31), Mindo (UMMZ 55516, USNM 193832, 193841, 193866), 10 km northwest of Nane-

gal Chico (USNM 193817), Nanegal Chico (UKMNH 108942-43, UPR-M 5090-91, USNM 193833, 193837-40), Río Blanco (USNM 193846, 193852), Río Mindo (USNM 193842-43), Río Toachi (USNM 193849), San Tadeo, near Mindo (USNM 193865), Tandayapa (BMNH 1972.736, CAS-SU 11388-89, USNM 193822, 193835-36, 193851-52). Province unknown: Miligali (USNM 193844-45).

Tentatively allocated to taxon: Ecuador: Imbabura Province, Carolina, 900 m (AMNH 50969, UMMZ 83656, 83658-60).

Atelopus mindoensis, new species

FIGURE 22

HOLOTYPE.—USNM 193554, from Mindo, Pichincha Province, Ecuador, 1200 meters, collected by Manuel Olalla, May 1959.

DIAGNOSIS.—A diminutive member of the *longirostris* group, most similar to *A. palmatus*, with

adult females usually shorter than 30 millimeters in standard length. Males usually shorter than 20 millimeters. First digit on forefoot almost entirely hidden in webbing; ventral surfaces unicolor, no spotting, dorsum with a broad yellowish brown band and reddish brown spotting and marbling.

DESCRIPTION.—Snout from above bluntly pointed, with canthus forming straight line from tip of snout to nasal eminence, from that point to corner of eye it forms a gentle inward curve. Snout and edge of canthus fleshy anterior to nasal eminence, but no fleshiness on canthus from nostril to eye, on eyelid, or on temporal region. Slight depression in center of snout, as consequence of fleshy margin; rest of dorsum of head flat. Snout from side prominent, projecting over lower jaw; nostril closer to tip of snout than eye, on raised area and directed laterally; loreal region vertical, gently rounded, no loreal depression anterior to eye. Temporal region with scattered pustules and spines, differing in number and prominence between individuals. Body liberally studded dorsally

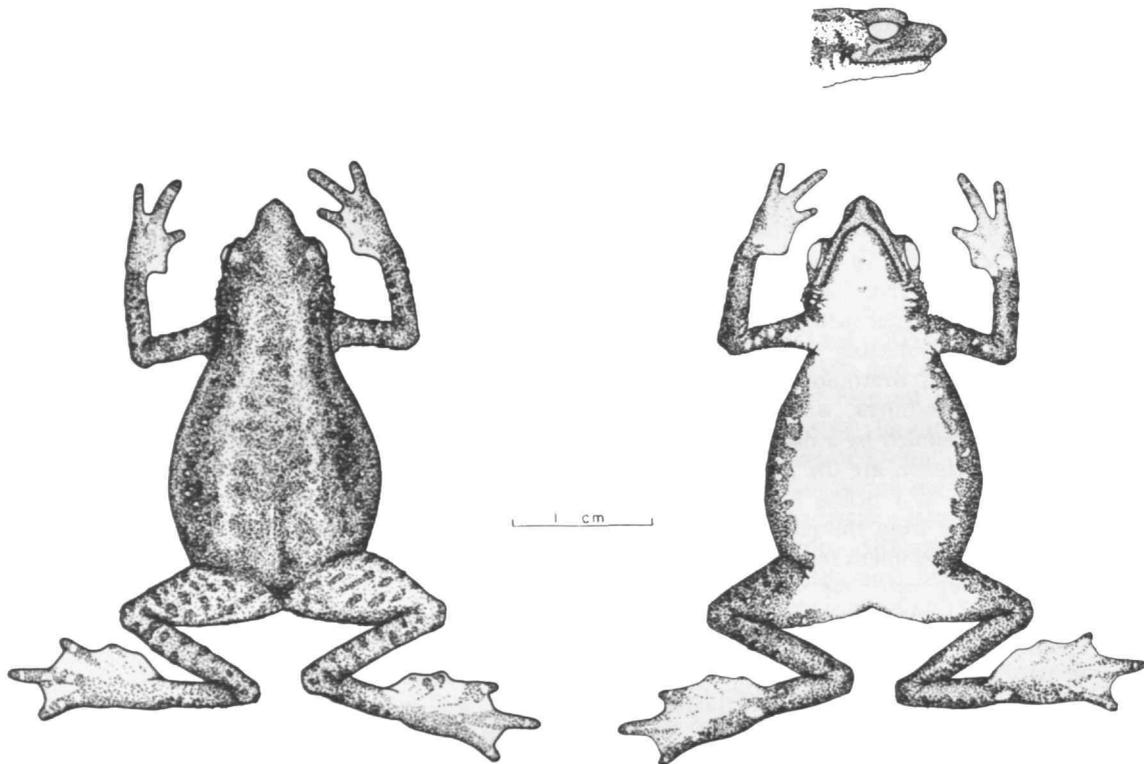


FIGURE 22.—Holotype, USNM 193554, of *A. mindoensis*, new species.

and laterally with tiny pustules widely scattered but at least in part organized into tracts; scattered larger, pointed, usually pigmentless, rounded pustules along dorsolateral line and laterally; limbs also studded with tiny spicules, concentrated in raised, fleshy areas along length of limbs.

Forelimb slender in females, shorter and heavier in males, forefoot has somewhat fleshy webbing, with first digit completely covered by it, second digit included by a border of web; webbing deeply incised between second and third and between third and fourth digits, with fleshy nature of webbing making it appear absent between these three digits. No subarticular tubercles on slightly fleshy ventral surfaces of digits; plantar tubercle low, rounded, almost indistinct.

Hind limb slender, heel reaches to points between posterior margin of eye and axilla when hind limb is brought forward along body; heels touch or slightly overlap when tibiofibulae are parallel to femora at right angles to body. Webbing on foot extensive and somewhat fleshy, with first toe almost completely indistinguishable within it, second and third digits completely and continuously webbed; fourth toe webbed to tip, but webbing is hardly more than a border on ultimate phalanx; full webbing on fifth digit. Ventral surface of foot is devoid of tubercles; fairly large, raised, prominent, pigmentless outer metatarsal tubercle present.

COLOR IN ALCOHOL.—Dorsal ground color rather light yellowish brown, forming broad band length of back, filled with reddish brown marbling, spotting, and vermiculation in younger individuals, practically totally obscured in older individuals, which tend to have back almost unicolor reddish brown. Some individuals have irregular stripe from eye to groin, bordered below by lighter stripe beginning at posterior margin of orbit and disappearing on sides. Sides are usually reddish brown, sharply distinct ventrolaterally from belly color; some specimens have series of clear, yellowish spots on lower sides. Venter is clear light yellow, usually quite transparent, with eggs visible in body cavity of ripe females. Ventral surfaces of limbs often completely invaded by dorsal color, but in some individuals yellow of belly is continuous with yellow

low color of foot. No spotting of any sort on throat, belly, or soles, except in one female with few light brown spots on chin. Side of head dark brown, including upper lip; area below eye often with light yellow crescent. Lower jaw entirely yellow.

HOLOTYPE.—The holotype conforms with the description given above for the species, where no variation is mentioned. Where alternatives appear in the species description, the holotype has the following characteristics: temporal region with about six large, white-tipped pustules and many scattered spicules. Heel reaches to the posterior margin of the head when hind limb is brought forward; heels overlap slightly when tibiofibulae are parallel to femora at right angles to body. Dorsum almost unicolor, with irregular, somewhat lighter area dorsolaterally that is vermiculated on its inner margins. Clear yellowish spots present on lower sides, some fused with light yellow ventral color. Eggs visible in body cavity. Ventral surfaces of limbs dark brown, with few scattered lighter spots. Light crescentic area present below eye, lower lip with dark brown margin, rest of chin and throat clear. Measurements (in millimeters): snout to vent: 29.0; snout to end of coccyx: 27.2; knee to knee: 22.0; tibiofibula: 11.3; head length: 8.6; head width: 7.7; eye diameter: 4.0; snout to eye: 5.2; interorbital distance: 3.8; width of eyelid: 3.9.

ETYMOLOGY.—The species name is derived from the name of the type locality, a most pleasant little town where Beatriz Moisset and I spent several delightful days in the field in 1965.

SPECIMENS EXAMINED.—The following are paratypes: ECUADOR: Pichincha Province; Milpe, 900 m (USNM 193562–63), Mindo (BMNH 1968.115, UKMNH 108944–45, UMMZ 131684, USNM 193556–59), Río Blanco, near mouth of Río Yambi, about 700 m (CAS 134204, USNM 193561), Río Lelia (AMNH 79462), region below Sigchos (MCZ 84200, USNM 193564), Río Toachi (USNM 193555, 193560). The following are not designated as paratypes: ECUADOR: Esmeraldas Province; Carondlet (USNM 193570), Alto Tambo (BMNH 1968.116, USNM 193571–72, UPR–M 5092). Pichincha Province: Mindo (USNM 193565), region below Sigchos (USNM 193569), region of Gualea (USNM 193566–68), Tandayapa (GOV 8696, USNM 193573).

Atelopus nepiozomus, new species

FIGURE 23

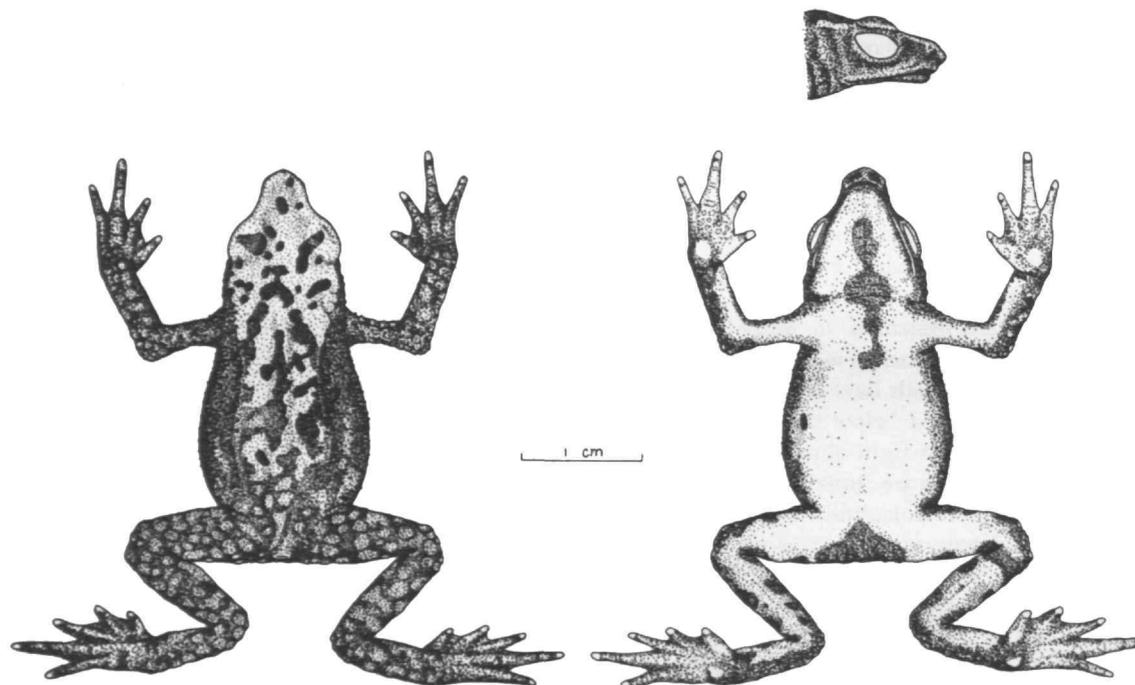
HOLOTYPE.—USNM 193543, female, from slightly above Suro Rancho (also called Gualacénita), a single house on the trail between Limón and Gualececo, approximately 16 kilometers airline west of Limón (which is now known as General Plaza), Morona-Santiago Province, Ecuador, approximately 3000 meters, collected by James A. Peters, August 23, 1962. See Figure 24 for map showing locality.

DIAGNOSIS.—A member of the *ignescens* group, very similar to *ignescens*, *bomolochos*, and *arthuri*, differs from all three in presence of scattered dark spots ventrally; dorsum with many low, rounded warts and pustules which may be spiculate; dorsum usually spotted and variegated with darker brown on lighter ground color; also very similar to *halihelos* (for contrasting characteristics, see diagnosis of *halihelos*).

DESCRIPTION.—Snout viewed from above roundly pointed, with canthus forming slight inward curve from tip of snout to nostril and then much deeper inward curve from nostril to eye; canthus fleshy

and raised, with nostril below it on a lateral prominence; snout area between canthi slightly depressed. Upper eyelid fleshy, followed by fleshy ridge from corner of eye to back of head. Frontal and occipital areas flat, markedly lower than fleshy margins of head. Snout viewed from side blunt, slightly projecting beyond lower jaw; nostril closer to tip of snout than eye, located on lateral eminence, directed laterally and slightly posteriorly, loreal region distinctly concave. Area behind eye to shoulder with raised, rounded warts, each of which may have several white-topped spinules on it. Dorsum and sides of body and legs with similar low, rounded warts (more prominent in females than in males), which may bear one to many whitish spinules or lack them entirely; generally more and larger warts laterally than dorsally. Chin, throat, belly, and lower surfaces of limbs usually finely wrinkled, but devoid of warts and spinules.

Forelimb slender in females, heavier in males; fingertips do not reach beyond body when leg is carried back along body. Webbing very reduced on forefoot, with first digit clearly distinguishable; webbing appears completely absent, but is actually very fleshy between digits at base; greatest extent of

FIGURE 23.—Holotype, USNM 193543, of *A. nepiozomus*, new species.

webbing between first and second digits, where it includes about half of first digit. First digit quite short, fourth longer than second, third much longer than fourth. Many low, rounded, fleshy tubercles on sole of forefoot and at digit articulations; outer metatarsal tubercle larger than others, but not pronounced or raised.

Hind limbs short; tibiotarsal articulation reaches to arm insertion or slightly farther when carried forward along body; heels do not overlap when tibiofibulae are parallel to femora at right angles to body. Webbing extends to tips of all toes, but is deeply incised between all except first and second, where it is complete and includes all of first toe; webbing forms distinct border on all toes, narrowing toward tips, giving tapered appearance to individual toe. Low, rounded tubercles at articulations and on sole; inner metatarsal tubercle low and rounded as others, outer metatarsal tubercle smaller but distinctly raised, pointed, and hard.

COLOR IN ALCOHOL.—Ground color of dorsum of legs and body pinkish gray, with marbling, spotting, and variegations of reddish brown. Ground color usually predominates, and in one individual darker area is confined to thin pencil stripe of color on vertebral column. Darker areas associated with warty swellings, so that where wartiness is heavier there is greater amount of darker marbling. Sides of head dark brown, with distinct and sharp color change at canthus and along dorsolateral ridge of head. In few individuals a poorly defined stripe of ground color from eye along dorsolateral margin to groin, usually not present or indistinct. Ventral surfaces of body yellowish to yellow-green, with some spots or streaks of dark brown usually present, most commonly on chin, throat, and chest; where thin, midline streak may broaden into one or several spots in tandem. Triangular, diaper-like patch extending from anus onto ventral surface of thighs. Dorsal surfaces of feet similar to body and legs, but about half of specimens have first three toes and first two fingers distinctly lighter than rest of foot, in some becoming quite yellow. Ventral surfaces of feet usually unicolor light yellow, but in some individuals may be dark spotted.

COLOR IN LIFE.—Dark greenish above with dark brown spots. Ventrally orange on thighs, arm insertions, and chin. Belly yellowish. Spots on throat and below anus very dark brown.

HOLOTYPE (Figure 23).—The holotype agrees with the species description above in all characters for which no variation is mentioned. For those characters which vary, the holotype is as follows: temporal and tympanic areas and sides of body with white-tipped spinules on warts, those on body not multiple on a single wart. Warts on legs lack white tips, except very near arm and leg insertions. Tibiotarsal articulation reaches point of insertion of forelimb; heels separated when tibiofibulae are parallel to femora at right angles to body. No definable dark stripe from eye to groin, whole side unicolor dark brown. Ventral surfaces of feet with dark areas. Measurements (in millimeters): snout to vent: 32.4; snout to end of coccyx: 29.3; knee to knee: 24.9; tibiofibula: 11.5; head length: 11.0; head width: 9.5; eye diameter: 4.8; snout to eye: 6.9; interorbital distance: 5.2; width of eyelid: 4.0.

REMARKS.—All of the specimens in the type series were collected during our 1962 field work, which was made up of a series of transects on the eastern slopes of the Andes. Since the routes followed were often only mule trails, it is not easy to identify stopping places and collecting localities where we worked during the week or so that a descent or ascent might take. Figure 24 shows all of our collecting spots during the final transect, which took us down one mule trail and back up a second a little farther south. Most of the names on the map are "tambos," or single houses which provide overnight facilities for mule drivers, and cannot be found on any other maps or in other gazetteers of Ecuador. They are, however, comparatively permanent, because they occur at approximately one "mule-day" intervals on the trail, and require a good-sized flat area for a house and a corral. Only when highways are open to towns such as General Plaza, Macas, and others in the lowlands, will the mule traffic stop, and these houses will revert to the forest.

ETYMOLOGY.—The species name is derived from the Greek word *nepios*, meaning "infant," and *zoma*, referring to a girded garment or the position of the girdle, i.e., the girded garment of an infant, as close as one can come to "diaper" in Greek. It refers to the patch of dark pigment that encloses the anus, upper thighs, and the posteriormost part of the venter of these frogs, which gives them the look of a diapered baby.

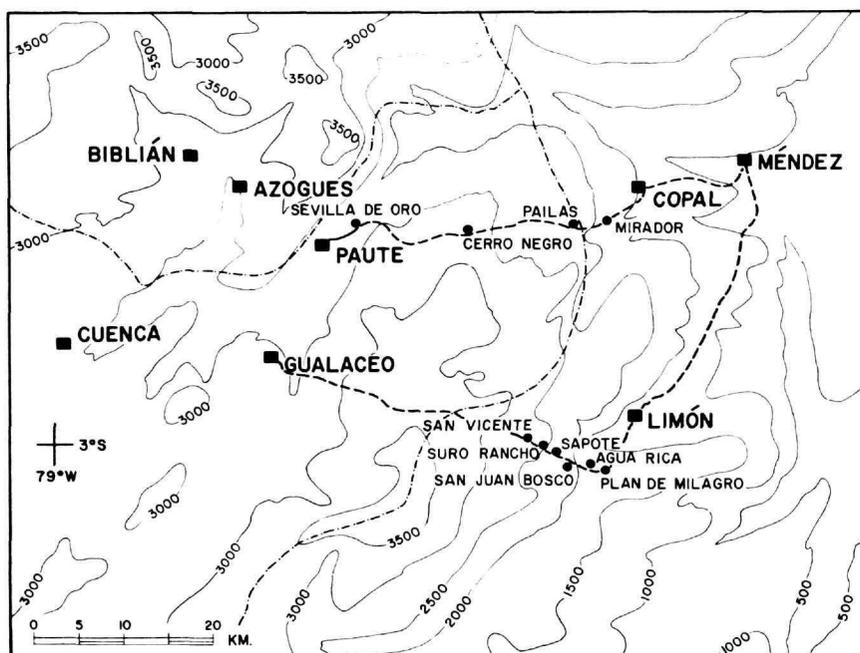


FIGURE 24.—Route of collecting transect made in August 1962, by J. A. Peters and party, showing localities along mule trails from whence material was obtained. Contour lines are in meters. (Based on the Mapa Geografico de Ecuador, published by the Instituto Geografico Militar, Quito, 1950.)

SPECIMENS EXAMINED.—The following are designated as paratypes: ECUADOR: Morona-Santiago Province; Cerro Negro, 3450 m (USNM 193544), near Pailas, circa 2150 m (USNM 193545), San Juan Bosco, 2000 m (BMNH 1972.735, AMNH 79463, USNM 193546–47), San Vicente, circa 3450 m (UKMNH 108946, USNM 193549–51), Suro Rancho, 3400 m (USNM 193548). The following were examined but are not considered paratypes: ECUADOR: Morona-Santiago Province; San Vicente, circa 3450 m (USNM 193552–53, JAP 7972–73).

Atelopus pachydermus (Schmidt)

FIGURE 25

Phrix pachydermus O. Schmidt, 1857:15 [type locality: "Neu-Granada"]; 1858:257, pl. 3: fig. 26.

A.[telopus] pachydermus.—Rivero, 1963:107; 1968:23.

Atelopus pachydermus.—Rivero, 1965:138.

HOLOTYPE.—In the Zoological Museum of Cracow, Poland. Present condition not known.

Schmidt (1858) gave additional information concerning the type locality, stating it to be "Westen von Neu-Granada, bei Bonaventura, in einer Höhe von 5000'."

DESCRIPTION.—Snout from above blunt, rounded, not projecting, distinct angle in canthus at nostril, canthi from nostril to corner of eye form straight line, angled slightly outward. Canthus and outer eye margin slightly fleshy, with distinct ridge from posterior corner of eye to end of head. Dorsum of head flat, without ridges, tubercles, or fleshy prominences; eye does not protrude dorsally. Snout from side slightly protrusive beyond end of lower jaw; nostril directed laterally, slightly below canthus; loreal region weakly concave; eye slightly overhung by fleshy edge of eyelid; temporal region without tubercles or spines, but in some individuals with glandular swellings. Dorsum of body broad, flat, with minute wrinkling and folding; in some individuals scattered, rounded, glandular prominences. Sides of body studded with rounded, glandular swellings, which are usually covered with

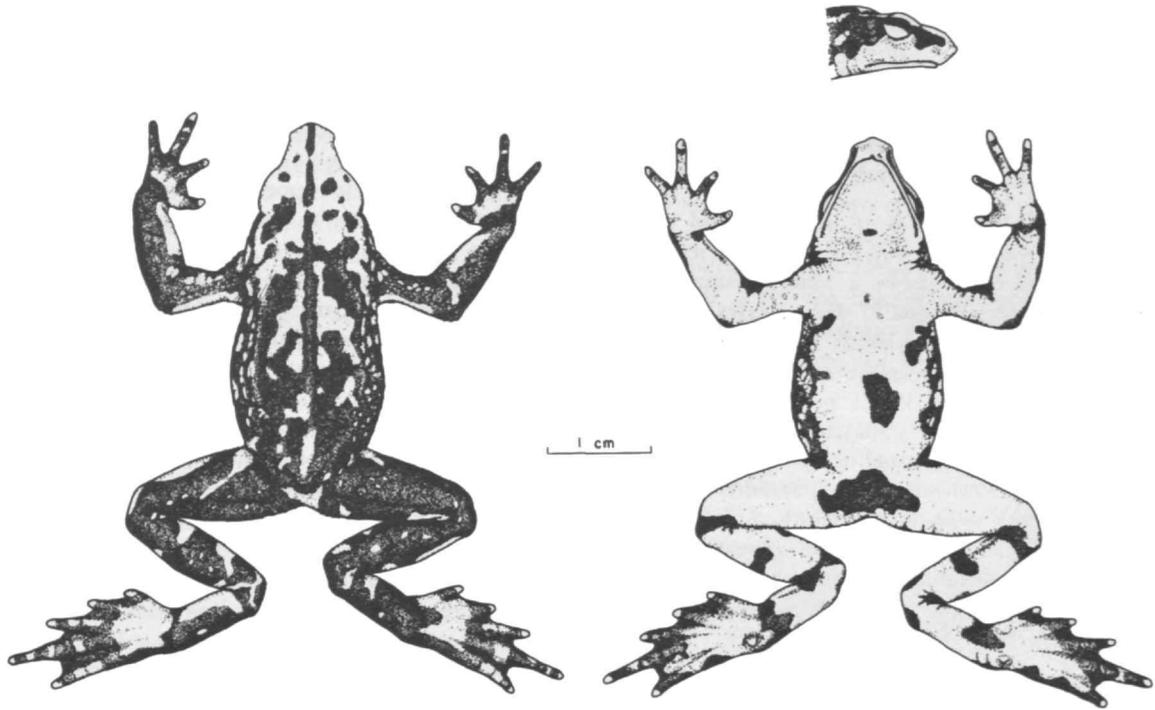


FIGURE 25.—A representative individual, USNM 193495, of *A. pachydermus* Schmidt.

several to many whitish spinules. Chin, chest, and belly wrinkled or lined, but without pustules.

Forelimb short, stout in males, more slender in females, forearm more fleshy than upper arm in both sexes; dorsum of arm with glandular swellings, rest smooth with wrinkles or folds. When arm is pulled back along body, digits reach level of hind leg perpendicular to body in females, not so far in males. Forefoot slightly fleshy, webbing very reduced, with all digits distinct and free; first digit more swollen than others, with horny excrescence from tip of digit to base in males, covering a raised hump of flesh, second digit with cornified area near base of digit. Subarticular tubercles absent, but palm with many raised glandular areas, often with pair at base of each of second and third digits; large palmar tubercle, less prominent plantar tubercle. Tips of digits slightly swollen.

Hind limb rather stout, occasionally glandular along femora, more often heavily wrinkled or folded. Tibiotarsal articulation reaches to points between end of head and arm insertion when car-

ried forward along body; heels do not overlap when tibiofibulae are parallel to femora at right angles to body. Entire foot with somewhat fleshy web, covering all but tips of first and second toes; extends to tips of other digits, but is deeply incised between them. No subarticular tubercles, no tubercles on sole, outer metatarsal tubercle low, rounded, somewhat indistinct, inner metatarsal tubercle ovate and low.

COLOR IN ALCOHOL.—The typical pattern for this species is shown in Figure 25. It may be described in general as: ground color or entire body cream-yellow, with irregular black vermiculations and spots dorsally, which may be so heavy as to cover head and back completely. Sides, venter, and legs also spotted, stippled, and vermiculated with black, with belly and undersides of limbs less spotted than elsewhere. Color patterns extremely variable.

COLOR IN LIFE.—The lighter dorsal areas are bright yellow. Many of the warts and pustules have white tops. The ventral surfaces are white in almost all individuals, but some may have orange

areas or spots, and some have red bellies, similar to those seen in specimens of *ignescens* from nearby localities.

HABITAT.—This high altitude species is extremely common in the vicinity of Papallacta, where they were found along the borders of the Río Papallacta, under rocks and stones in moist, spongy, runoff areas.

VARIATION.—All species of *Atelopus* tend to be variable in coloration, but the available material of *A. pachydermus* shows a striking amount of variability. Figures 26 and 27 show a series of adults from the immediate environs of Papallacta, arranged to show the decrease in amount of light pigment in the series. While no individuals were taken in the region of Papallacta which lack the dark pigment entirely, some of the specimens from the region of Oyacachi are apparently entirely free of any dark spotting and mottling, and in life must present a striking golden appearance. In addition to the variation in the amount of pigment

present in adults, there is a distinct ontogenetic color change. Individuals 27 millimeters or less in body length lack the strong contrast between the dark and light areas seen in adults. The dorsal areas that presumably will be yellow in adults are dark gray or light brown in juveniles, and the darker areas are not strongly differentiated from the lighter. Some juveniles appear almost totally black dorsally. Ventral color in the juveniles is the same in adults.

REMARKS.—Rivero (1965:138; 1968:23) has discussed the use of the name *Atelopus pachydermus* (Schmidt) for the population described here. He examined the AMNH material from Oyacachi, and tentatively assigned it to this taxon, and I have followed him in this action. As Rivero pointed out, however, there are problems involving the type locality of Schmidt's taxon. The holotype of *pachydermus* was said to have come from above Buenaventura, at 5000 feet, presumably in the province of Valle, on the western slope in Colombia. All



FIGURE 26.—A series of specimens from the environs of Papallacta selected to show the variability in dorsal pattern and distribution of colors in *A. pachydermus*. Numbers refer to field series, and all have been recataloged.

of my material is from the eastern slope in Ecuador, almost entirely at altitudes considerably above that of the type locality. I consider it most unlikely that any *Atelopus* species is capable of maintaining a genetic continuum between these two areas, and if the existence of a species answering the description of *pachydermus* in the region of the type locality is verified, my material will probably need a new name. I continue to use the name *pachydermus* here for two reasons. First, the species has never again been taken at or near the type locality, nor has anything resembling it shown up there. It is entirely possible that the type may have come from the eastern slope, not the western, of Colombia, with either an erroneous locality given in the description by Schmidt, or, as Rivero (1968:23) suggested, there is a village called Buenaventura on the eastern slopes of Colombia. Second, my specimens do fit the original description fairly well, and the series includes specimens very similar to the holotype in coloration. They are found at comparatively high altitudes in northern Ecuador, and there seems to be a good likelihood that the same species could range into Colombia. The name

is certainly appropriate to my specimens, and I use it for them temporarily, until further evidence accumulates on the taxon.

A series of specimens from the collections of Gustavo Orcés-V. (GOV 8698-700) are recorded as collected at Loja, Ecuador, but I am sure this is an error in the transcription of the data, perhaps made by me when transferring that collection to the National Museum. The series is unicolor light golden, and is identical with material from Oyacachi. I do not believe the same taxon, and the same striking variation in pattern, also occurs in Loja, and I have not included that locality in the following list.

SPECIMENS EXAMINED.—ECUADOR: Napo Province; 2 km E of Chalpi, 2755 m (USNM 193520-21), Oyacachi, 3300 m (AMNH 20505-21, BMNH 1972.732-733, CAS-SU 10348-50, 134200, JAP 3791, MCZ 84201-02, USNM 193494, 193522-33), Pueblo Viejo, Oyacachi (AMNH 20492-93), Papallacta and environs, 3150 m (KU 117876-79, 142950-56, UMMZ 131020-21, UPR-M 5088-89, USNM 193495-518).

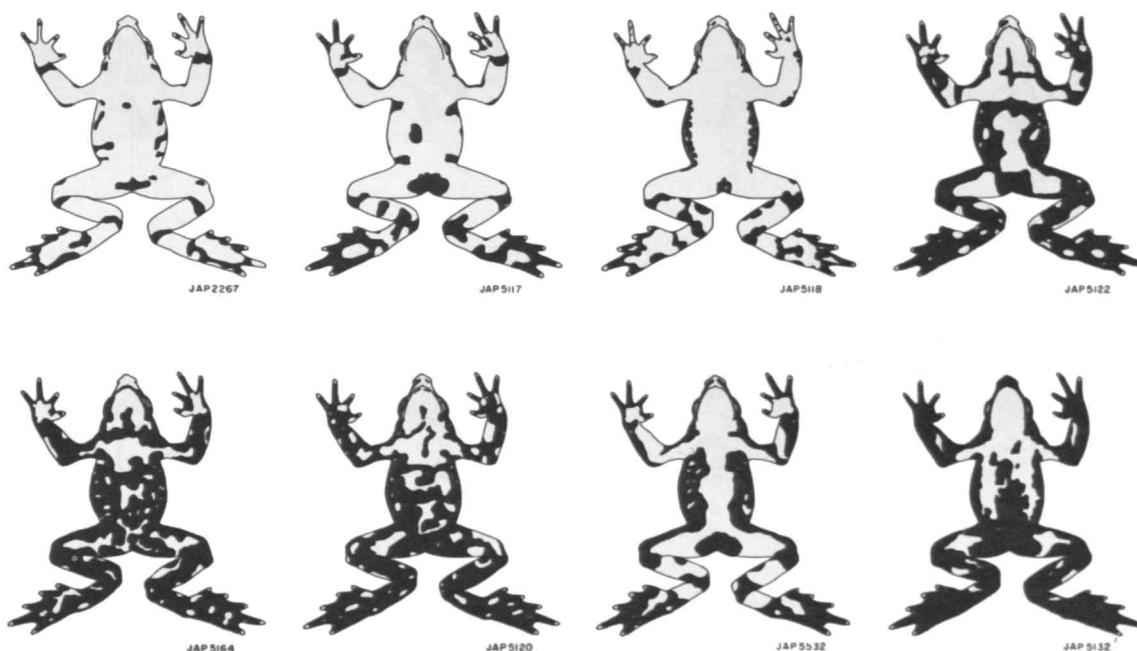


FIGURE 27.—Ventral view of same series as in Figure 26.

Atelopus palmatus Andersson

FIGURE 28

Atelopus palmatus Andersson, 1945:12, fig. 4 [type locality: "Río Pastaza, Ecuador. 1000 m"].—Rivero, 1963:110; 1968:21; 1969:142.

SYNTYPES.—Stockholm Royal Museum number 1908, 5 individuals.

DESCRIPTION.—Snout from above with pointed, projecting tip; canthus forms straight line from snout tip to level of nostril and then forms inward curve from nostril to corner of eye. Snout, canthus, and eyelid raised, but weakly fleshy; bony ridge from posterior corner of eye to corner of head, ending in raised boss. Dorsum of head finely shagreened, forming a plane surface, eyes slightly raised above plane. Snout from side protrudes well beyond both upper lip and lower jaw, may be slightly concave laterally, and may curve slightly downward at tip, giving "hooked" appearance. Nostril lateral, slightly below canthus, loreal region slightly concave. Vertical ridge joins dorso-

lateral ridge behind eye. Side of head shagreened, without raised tubercles or glandular areas. Dorsum and sides of body lightly shagreened; vertebral column forms indistinct ridge. Chin and belly finely shagreened or lightly wrinkled and folded.

Forelimb long, slender; forearm heavier than humeral region, dorsum lightly studded with small pustules or finely shagreened, ventral surfaces smooth or finely wrinkled. Forefoot with webbing enclosing all but tip of first toe, weakly developed on other digits. Subarticular tubercles absent or very weakly developed, palmar tubercle large, prominent, no plantar tubercle. Edge of prepollex with horny excrescence in males.

Hind limb slender, lightly pustulate along dorsum of upper leg, smooth elsewhere. Tibiotarsal articulation reaches to points between nostril and anterior border of eye when carried forward along body; heels touch or overlap when tibiofibulae are parallel to femora held at right angles to body. Webbing extends to tips of toes, with first and second digits almost totally obscured; webbing rather deeply excised between other toes, reaches

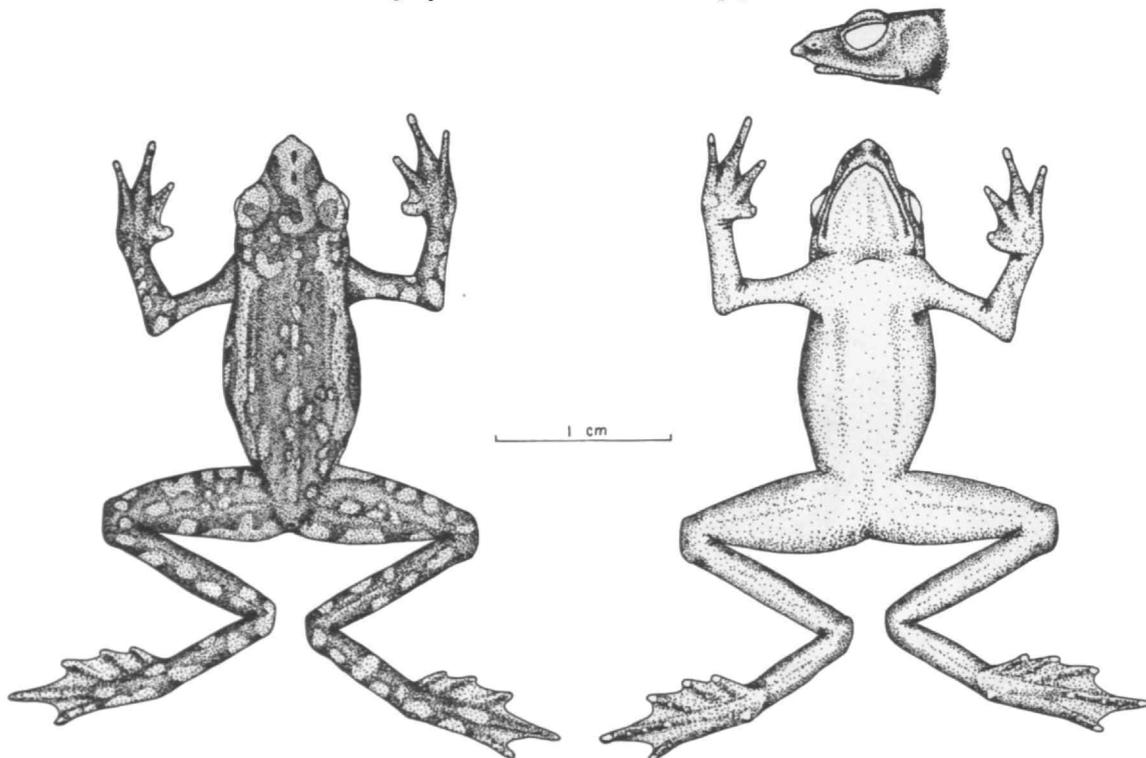


FIGURE 28.—A representative individual, FNHM 36657, of *A. palmatus* Andersson.

tip of fourth toe as a fringe. Subarticular tubercles weak and occasionally indistinct, outer metatarsal tubercle prominent, inner metatarsal tubercle absent.

COLOR IN ALCOHOL. — Dorsal ground color chocolate-brown, dorsum of head spotted and variegated in light gray, usually with dorsolateral streak or series of spots of same color from eye to groin, scattered spots with irregular margins on back. All light gray areas bordered with narrow dark brown to black margin. Ground color extends down side of head and body about halfway, with lips, shoulder, and lower sides as well as all ventral surfaces unicolor light brown to yellow. Limbs as body dorsally and ventrally; dorsum of first digits on both fore and hind foot usually yellowish, with no brown pigment dorsally.

COLOR IN LIFE.—“Dorsal surfaces dark brown with bright green spots. Flanks orange-yellow. Ventral surfaces, including inner 2 digits of fore- and hindlimbs, deep yellow. Groin bright orange-yellow. Iris black with minute greenish yellow flecks and ring around pupil.” (Taken from field notes on KU 122544, made by W. E. Duellman.)

REMARKS.—Rivero (1969:142) has examined the syntypes of *A. palmatus*, and he indicated that the species was valid, but closely resembled *A. planispinus*, a larger species from the slopes of Mt. Sumaco. I agree with this conclusion and, as indicated by the list below, have found a good series of specimens in the various museums. Rivero mentioned that the posterior margin of the frontoparietal and the upper margin of the suprascapulas are raised and prominent in some of the syntypes, but this is not evident in the series I have examined except in individuals either dried or preserved in a solution with too high an alcohol content.

Little is known about the ecology of this species. A specimen collected by W. E. Duellman was taken on the margin of a small stream during daylight hours.

SPECIMENS EXAMINED.—ECUADOR: Napo Province; El Chaco, Upper Río Quijos, 1454 m (USNM 193541–42). Pastaza Province; Abitagua, 1200 m (UMMZ 90367), Baños (FMNH 28079), Hacienda San Francisco, on Baños-Mera trail (FMNH 36657, 152136), Mapoto (FMNH 36687), Puyo (FMNH 28078), Sarajacu (AMNH 33891–92), southern slope of Cordillera Dué above Río Coca, 1150 m

(UKMNH 122544), Río Azuela, 1740 m (UKMNH 142957–64).

Atelopus planispinus Espada

FIGURE 29

Atelopus planispina Espada, 1875:148, pl. 2: figs. 1–2 [type locality: “San Jose de Moti, Ecuador”].

Atelopus longirrostris [sic].—Espada, 1875: pl. 2: fig. 1 [see below, in “Remarks”].

Phryniscus cruciger.—Boulenger, 1882a:154 [a questioned synonymy].

A.[telopus] cruciger.—Nieden, 1926:84 [a questioned synonymy].

A.[telopus] planispinus.—Rivero, 1963:107.

SYNTYPES.—Twenty-eight specimens, MM 212, Museo Nacional de Ciencias Naturales, Madrid, Spain.

DESCRIPTION.—Snout from above with rounded, protrusive tip, with sharp angle at nostril; canthus rostralis from nostril to angle of eye forms straight line angling outward from anterior to posterior; no heavy fleshy margin on canthus. Dorsum of head flat, in same plane as broad, flat dorsum of body; bony ridge from corner of eye to end of skull above tympanum, ending in boss; head shagreened with tiny spines, heavier on eyelids. Snout from side overhangs lower jaw, ending in heavy point, which may be bent somewhat downward, i.e., “hooked,” nostril laterally directed, below canthus, loreal region vertical, does not form concave area. Eye slightly overhung by moderately fleshy margin of eyelid. Upper lip and head behind eye spinose and pustulose. Entire body finely speckled with tiny spinules visible under high power of microscope; on sides and in groin spines are much more prominent and pustules are also present.

Forelimb slender, elongate, shagreened with spinules and spines. When forelimb is pulled back along body, palm reaches vent. Hand fleshy; first digit enclosed in fleshiness except for its tip; other digits free or with slightly fleshy border, not webbed. Second digit shorter than fourth. Subarticular tubercles absent or very ill defined, larger palmar tubercle, no tubercle at all at base of first digit.

Hind limb slender, covered with spinules and scattered spines, not pustulate. Tibiotarsal articulation reaches to points between nostril and pos-

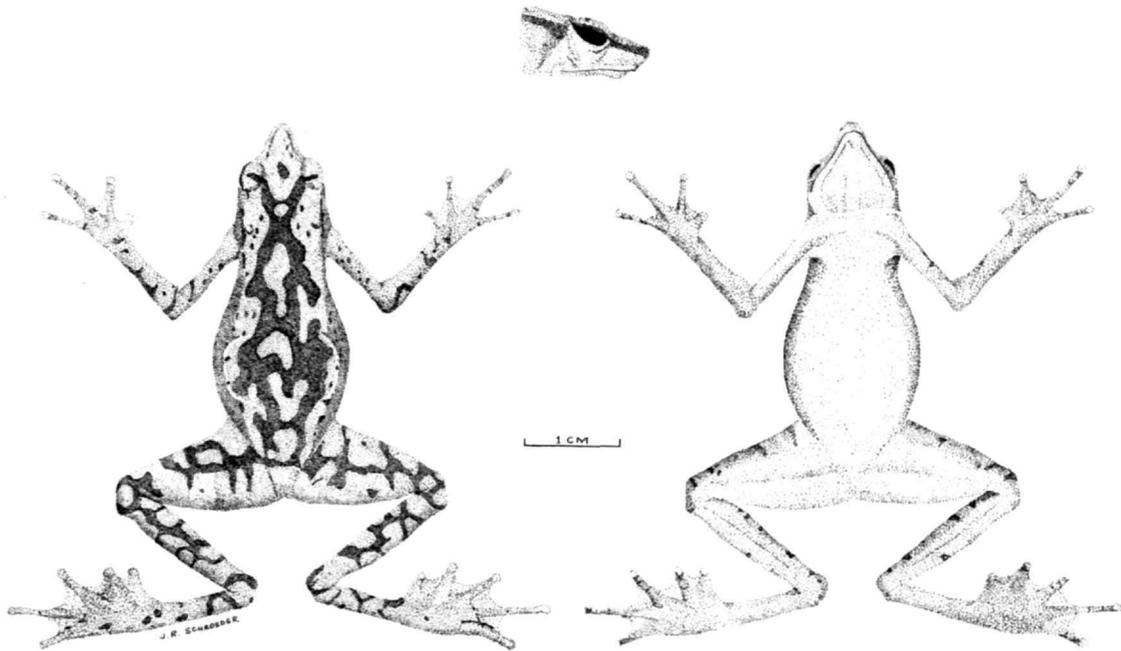


FIGURE 29.—A representative individual, AMNH 22198, of *A. planispinus* Espada.

terior margin of eye when carried forward along body. Heels overlap when tibiofibulae are parallel to femora at right angles to body. Entire foot fleshy, webbing almost entirely encloses first and second toes; webbing extends to tip of other toes as fringe, but is deeply incised between them. Sub-articular tubercles weakly defined, outer metatarsal tubercle forms rounded hump, inner metatarsal tubercle obscured by fleshiness of first toe.

COLOR IN ALCOHOL.—Dorsal ground color light tan, with highly vermiculated markings of light to dark brown. Dorsolateral region usually solid ground color with scattered small dark spots, rest of dorsum very irregular and sometimes so heavily marked with dark brown that ground color forms isolated spots. Lower sides, chin, chest, and venter usually without spots, yellowish white (one juvenile has brown markings on chin and throat). Ground color of limbs tan, with dark brown bars or vermiculations which do not extend onto yellowish white lower surfaces of limb. Outer margins of soles of feet dark brown, inner parts yellowish white.

SYNTYPES.—The 28 syntypes in the Madrid Museum are badly faded, and a few appear to have been dried. Most of them have lost all signs of pattern, but one small male still retains most of its color, and it is possible to see enough parts of the pattern on other individuals to be sure that the more recent specimens identified here as *planispinus* belong to the same species. Insofar as they can be determined on the type series, the characters given above for the species as a whole are accurate for the types. Characters such as spicules and spines, or degree of fleshiness, could not be determined on the syntype.

REMARKS.—The type locality for this species, given as "San José de Moti" by Espada, is apparently the town in Napo Province now called San José Nuevo. The United States Board on Geographic Names in their volume on Ecuador (1957: 155) gave a reference to San José de Mote, with a cross reference to San José Nuevo, at 0°26'S, 77°20'W, which is on the lower northwestern slopes of Mount Sumaco, the only place from whence I have seen specimens. The town itself is quite low,

and it is unlikely that the type series originated there. I suspect the 28 specimens came from the slopes of Mount Sumaco, as do the AMNH specimens. I doubt also the reference to the "top" of Sumaco for AMNH specimens, since that is at 3900 meters, an altitude higher than any other species of *Atelopus* in Ecuador except *ignescens*, and much higher than any other species in the *longirostris* group, which, as pointed out above, tends to be found at lower, warmer altitudes.

Espada (1875, pl. 2: figs. 1, 2) illustrated what he identified in the legends for the Plate 2 varieties of *A. longirostris* (sic), but did not present a figure of his own new taxon, "*A. planispina*." If one reads the section termed "Observ." on page 154 of Espada's text, one discovers that Espada considered *longirostris* and *planispinus* to be closely related, and in fact he thought of the two samples he had as variants of *longirostris* for some time, until he decided that "son verdaderamente dos especies, muy afines si, pero distantas." Since his figure 1 on Plate 2 is the same taxon I am calling *planispinus* on the basis of the AMNH specimens from Mount Sumaco, I believe that the plate legend did not get changed when Espada decided to give

the new taxon the name "*planispina*" rather than to continue to regard it as a variety of *longirostris*. The species shown in Plate 2; figure 2, in Espada, is probably actually *A. longirostris*, although the figure is not detailed enough to be certain. Espada did have specimens of *longirostris* from Nanegal in his collection (1875:159).

This species and *A. halihelos* are apparently restricted to isolated mountain masses to the east of the main Andean chain in Ecuador. It is unlikely that either of them are found in the lowland areas surrounding these masses, because other wide-ranging species of *Atelopus* are found there.

SPECIMENS EXAMINED.—ECUADOR: Napo Province; San José de Moti (MM 212—syntypes), Top of Sumaco Mountain (AMNH 22193, 22195–97, 22199–200, USNM 193960), side of Sumaco Mountain (AMNH 22300–301).

Atelopus pulcher pulcher (Boulenger)

FIGURE 30

Phryniscus pulcher Boulenger, 1882:154, pl. 13: fig. 2 [type locality: "Chyavetas, Peru" perhaps the same as Chayahuitas, Peru, according to Rivero, 1968:19].



FIGURE 30.—A syntype, BMNH 1947.2.14.80, of *A. pulcher* Boulenger.

Atelopus pulcher.—Boulenger, 1894:375.—Peracca, 1904:22.—Rivero, 1968:107.

Atelopus spumarius.—Rivero, 1968:19.

Atelopus spumarius spumarius.—Duellman and Lynch, 1969:232.

SYNTYPES.—Four individuals in the British Museum (Natural History), and USNM 193574.

DESCRIPTION.—Snout from above rounded from nostril to nostril, canthus forms a straight line from nostril to eye, little or no fleshy area on snout region or on canthus. Dorsum of head flat, smooth, slight knob at corner of skull. Snout from side very slightly protrusive beyond upper lip and lower jaw; nostril directed laterally. Loreal region vertical; upper eyelid slightly fleshy, overhangs eye; upper lip not fleshy; temporal and tympanic areas smooth or very lightly wrinkled and shagreened. No tubercular areas on head, body, or limbs. Dorsum and sides of body lightly wrinkled, belly wrinkling somewhat more pronounced.

Forelimb slender and slightly wrinkled, forearm usually thicker than humeral region. When forelimb is drawn back along body, palm reaches thigh. Palm of hand fleshy; first digit distinct, with tip of digit free of fleshy webbing; other digits entirely free of webbing; subarticular tubercles very indistinct; palmar tubercle very large, rounded.

Hind limb slender, smooth or finely wrinkled, under surfaces of thighs below anus with markedly wrinkled and somewhat pustulate area, usually distinctively colored. Tibiotarsal articulation reaches points between anterior and posterior margins of eye; heels touch or overlap when tibiofibulae are parallel to femora at right angles to body. Entire foot somewhat fleshy, with first digit entirely hidden in webbing, second with only its tip protrusive, other three digits webbed to tip, on fourth chiefly as fringe. Subarticular swellings present; outer metatarsal tubercle present but small.

COLOR IN ALCOHOL.—Dorsal ground color greenish yellow, with dark brown vermiculations and spotting more or less symmetrically distributed on head, back and sides; upper lip yellow, with a fine brown line along margin. Belly and chin yellow, with small rounded brown spots primarily located posteriorly. Limbs barred above with dark brown, yellow below with brown spotting. Soles of feet and area just below anus flesh colored.

COLOR IN LIFE.—Dorsal ground color yellowish green, with jet black spotting and striping. Soles

of feet bright red, with area on venter that is flesh colored in alcohol also bright red. In some individuals the entire ventral surface is red.

REMARKS.—Rivero (1968:19) discussed at length the two taxa *A. pulcher* Boulenger and *A. spumarius* Cope, and finally concluded, with doubts based on Cope's inadequate description of his type, that they were synonymous. I have not accepted this action in my work for the following reasons. First, *A. pulcher* Boulenger is a well-defined, easily recognized species, with a good figure accompanying the original description, and with type material available for comparisons. As a consequence, the name has been used and the species recognized by all workers in eastern Peru and Ecuador since Boulenger's Catalogues were published. Second, Cope's species is inadequately described; no figure was published to show what in the world he meant when he wrote about "aggregated annuli of greenish yellow . . . the appearance of green foam," and the holotype has never been located. The substitution of a poorly described, inadequately characterized taxonomic name for a well-described, clearly defined one with type material available, and which has been in wide use for 80 years, seems to me to be an inadvisable taxonomic practice, and I hope we can return herewith to the widely recognized name with only a minimum of use of the substitution. This does not seem to me to require more than a recognition by herpetologists that *A. spumarius* is clearly a dubious name until such a time as the holotype is rediscovered, and, as such, should not be applied to a known species until the doubts are resolved. This would require that the subspecies described by Rivero (1968:23) be known as *Atelopus pulcher andinus* Rivero.

Rivero has also discussed (1968:20) my views that high altitude records for this species are undoubtedly incorrect. He pointed out that he could recognize differences between specimens supposedly from Riobamba, a city in the inter-Andean highlands at 2800 meters, and the lowland material from the Upano Basin. Savage (1960:14) has discussed the validity of Riobamba as the source of certain AMNH specimens, and I follow him in not accepting Riobamba as a valid locality for any lowland species until verification in the form of newly collected specimens has been made. The AMNH specimens were received from H. Feyer, and his "Riobamba" records of lowland species

have been causing problems in Ecuadorian herpetology for years. It seems clear that Feyer, with his residence in Riobamba, purchased specimens from any seller, including mule drivers coming up from the Amazonian lowlands on their regular trips, carrying a few frogs and snakes along to sell to the "gringo," who then used "Riobamba" as the origin of the specimens.

The specimens mentioned by Rivero (1968:20) from Chancha, Chimborazo Province, are from Normandia, in Morona-Santiago Province. This locality is discussed by Savage (1960:13), who located it at 1300 meters on the trail between Macas and Riobamba. This is within the known range of the species.

Duellman and Lynch (1969:232) described and figured a single presumed tadpole of this species, which was collected in the Río Puyo in 1969. They followed Rivero in the use of *spumarius* for the species, as did McDiarmid (1971:39).

The species *Atelopus tricolor* Boulenger (1902:397) is close to *A. pulcher* in its characters. I have had an opportunity to examine the syntypes, however, and they appear to me to represent a distinct taxon. One of the syntypes is now in the USNM collection, through the kindness of the British Museum (Natural History) (USNM 193575).

Rivero (1968:19) has discussed the spelling of the type locality in detail, and concluded that it was very likely that the Peruvian village called Chayahuitas, at 5°5'S, 76°10'W, was the original source of the type material. Since Chyavetas has never been located, his argument has considerable validity, and I have indicated that the village he located is probably the legitimate type locality.

SPECIMENS EXAMINED.—ECUADOR: (AMNH 17433–38, 17447). Morona-Santiago Province; Chancha, Normandia (AMNH 16695–712), Cutucú Cordillera (AMNH 33913–15), Macas (AMNH 21492–94, USNM 65487–90), Miazal (GOV S940, JAP 3843), Limón (CAS 134202–03, JAP 6966, 7520, UMMZ 131022–23, USNM 193479–90). Pastaza Province; "Baños and Canelos" (AMNH 16713–15), Canelos (MCZ 17927–28), Puyo (FMNH 28078), 2½ km southeast of Puyo (JAP 1937–38), Río Oglan (GOV S939), Veracruz (JAP 6105, UKMNH 120480–85).

PERU: Chayahuitas (BMNH 1947.2.14.80, USNM 193574, syntypes of *A. pulcher*).

Present Position of Taxa Formerly Assigned to *Atelopus* In Ecuador

There is a single species originally described in the genus *Atelopus* from Ecuador that is no longer considered to belong to that genus. *Atelopus festae* Peracca is now considered to belong to the genus *Rhamphophryne* (Trueb, 1971:22). A second species, *Atelopus minutus* Melin, although not originally described from Ecuador, has been collected in the country several times. It was recently transferred to the genus *Dendrophryniscus* by McDiarmid (1971:40).

Incertae Sedis

Atelopus longirostris marmorata Werner

This taxon was described by Werner in 1910, page 600, from "Ecuador," without more detailed information on the type locality. He noted that the females in his collection appeared different from the males of *longirostris*, and used the trinomen above for them. Nieden (1926:81) included the taxon in the synonymy of *Atelopus longirostris*, and the few citations since that time (Rivero, 1963; Cochran and Goin, 1970) accepted Nieden's action as having done away with the taxon. Careful examination of all of Nieden's work in this volume of *Das Tierreich*, however, shows that he included *all* trinomials in existence prior to his work as synonyms of a binomial, and then mentioned those he considered to be recognizable in the text below the synonymy I find only three subspecies mentioned in the entire volume, all in the text material. One of these is *marmorata*. It is, therefore, not particularly valid to cite Nieden as the authority for the synonymy of *marmorata* with *longirostris*. I think it entirely possible that Werner had specimens of a completely different species in hand. Since *elegans* occurs on the western slopes in Ecuador, and may actually be sympatric with *longirostris* in part of its range, I would suggest that Werner may not have recognized specimens of *elegans* among his *longirostris* material. Unfortunately, the type specimens were destroyed during World War II, and *marmorata* becomes a *nomen dubium*.

Zoogeography and Evolution

Rivero (1963:112) has remarked, "Frogs of the genus *Atelopus* seem to be very sensitive to environmental factors." This is certainly true of Ecuadorian species, particularly at altitudes above the subtropical zone. The Ecuadorian terrain makes exploration by herpetologists difficult, and not too much work has been done on the outward facing slopes of the Andes as a consequence. Access to areas between 1500 and 3300 meters has always been and still generally is available only on foot or horseback, although road construction on both east and west slopes continues to make more areas accessible by car. Most of my personal collecting efforts in Ecuador have been focussed on these slopes. I have spent comparatively little time in the Pacific lowlands, and even less in the Amazonian rain forest. Herpetologically, the latter has been the most popular and thoroughly explored area in the country, and, while it continues to produce both novelties and surprises, it still does not hold the same promise for investigation of ecological and evolutionary phenomena as do the Andean slopes.

In 1958-1959 I made a series of seven transects from the inter-Andean valleys to the Pacific lowlands, and in 1962 my group made five transects on the eastern slopes, usually, although not always, penetrating to the Amazonian lowlands. Such transects perforce follow available routes, and of the total of twelve transects, five were by mule and on foot, six were by road in truck or Landrover, and one was by rail. Since the routes taken were either mule trails several hundred years old, or roads that follow such old trails and replace them, it is to be expected that each trail would be separated by some distance and usually some fairly substantial physical or physiographic barrier from the next trail, since *arrieros* follow paths of least resistance, and do not develop and follow duplicate trails ending at the same place very often (except as smugglers). The physiographic barriers are deep river valleys, sheer cliffs, or too heavily dissected slopes, all of which can and do act as biological barriers to species movement equally well. In addition, rain shadow slopes, where the vegetation and moisture available change radically within a few thousand feet, occur on both east and west slopes, and represent a major biotic barrier to horizontal migration of mountainside species. Since these va-

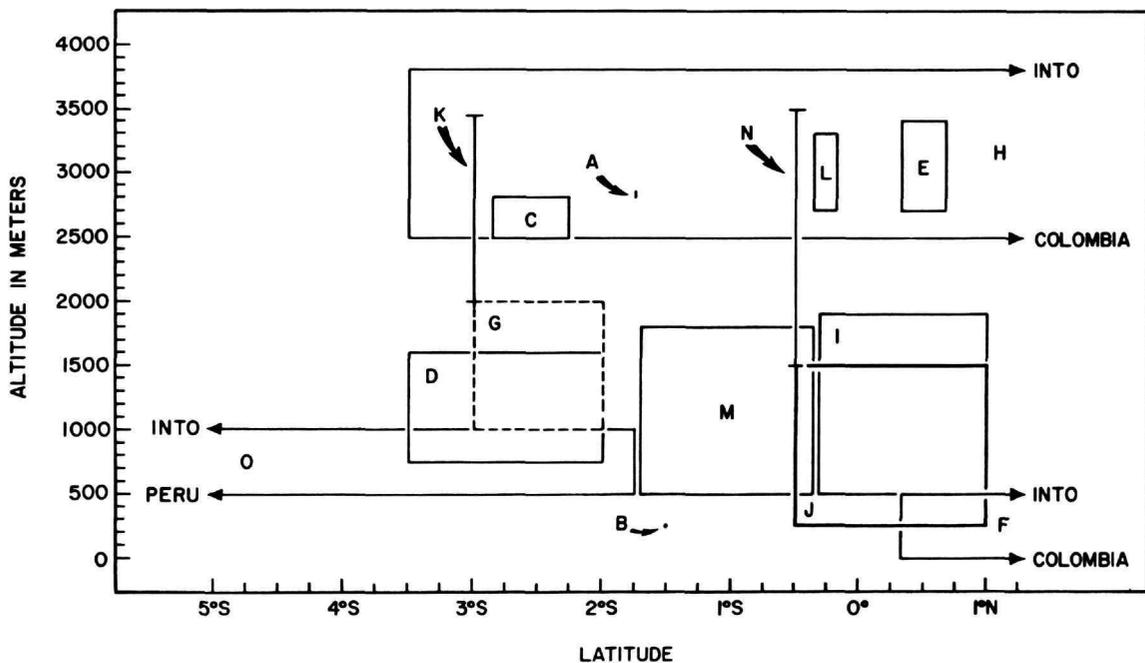
rious types of barriers are common, and are most often encountered between the traditionally used trails, one would expect each transect to produce different taxa, each evolving in an isolation produced by the barrier of altitude on one hand, and the many horizontal barriers mentioned above on the other hand. This proved to be particularly true of frogs of the genus *Atelopus* and lizards of the genus *Proctoporus*. Since representatives of both genera are fairly often found even if the total collecting time available is slight, they become good indicators of evolutionary patterns, effects of isolation, adaptive radiation, and other phenomena often associated with the study of insular faunas. In point of fact, mountains such as the Andes of Ecuador can be considered "continental islands," and many of the phenomena long discussed by students of insular biology are equally observable there, with the added advantage that the mountains are not dependent upon waifs and drifters for replenishment of the supply of evolutionary materials.

The taxa in the genus *Atelopus* lend themselves to the study of these phenomena because of the sensitivity to environmental factors already noted by Rivero. But, although they are sensitive to, and often limited by, very slight environmental changes, they are also capable of adaptation and divergence, which permits them to conquer new environments. Suitable habitat for the taxa in the lowlands of Amazonian Ecuador as well as in the lower altitudes on the Pacific side appears to be continuous, with few barriers to gene flow, and lowland species tend to have a considerable latitudinal range. *A. pulcher* ranges throughout the southern half of Amazonian Ecuador and a considerable distance in Peru, from whence it was originally described. It stops at about the Río Pastaza, and is replaced by *A. palmatus*, the northern limit of which is currently unknown. *A. elegans* is a lowland species on the west side of the Andes in Ecuador, and is found north well into Colombia and south to the point where the wet areas are replaced by the dry coastal scrub, under the influence of the Humboldt Current. Figure 31 is an attempt to show how the situation changes when the species found on the slopes at slightly higher altitudes are examined, and the opportunities for horizontal migration are diminished by the multiplicity of barriers. The extremely narrow distribu-

tion of the species found at altitudes above 2000 meters is in part an artifact of the collecting opportunities, which are restricted to a few hundred yards laterally to the trails, but it is fairly certain that there is a high degree of endemism on the higher slopes, and it is very likely that the endemic species are totally allopatric. Finally, after an altitude sufficient to permit the inter-Andean highlands to be reached, the picture is reversed. The highly successful species *A. ignescens* is capable of living at very high altitudes under most inhospitable conditions. As a result, it is the most widespread amphibian species in the Andean highlands, ranging from well into Colombia practically to the Peruvian border. The ability to live in paramo and subparamo climates has eliminated all physical barriers to movement by the species, and it is

ubiquitous over a considerable range. It is the only species that may in several cases be sympatric with those species with restricted ranges on the outer slopes. I have found *A. ignescens* within 2 to 3 kilometers of populations of *A. pachydermus*, and it appears that the same is true for *A. bomolochos*, much farther to the south. *A. ignescens* is, of course, sympatric with *A. bufoniformis*, which has been taken as high as 3400 meters, and is known from both slopes of the Andes, but only in the most northern provinces of Ecuador. *A. bufoniformis* is the end point in the evolutionary sequence discussed below.

While the evolutionary sequences are not entirely clear, and the evidence used here is primarily morphological and zoogeographic and thus could be easily disproven by data from cytological, ge-



- | | | |
|----------------|----------------|---------------|
| A ARTHURI | F ELEGANS | K NEPIOZOMUS |
| B BALIOS | G HALIHELOS | L PACHYDERMUS |
| C BOMOLOCHOS | H IGNESCENS | M PALMATUS |
| D BOULENGERI | I LONGIROSTRIS | N PLANISPINUS |
| E BUFONIFORMIS | J MINDOENSIS | O PULCHER |

FIGURE 31.—A diagrammatic representation of the known distribution patterns of the species of *Atelopus* in Ecuador. Each square (or line) is based on known extremes, and therefore may well include areas from whence a particular species is not known. In each species a complete rectangle is shown, although this is not easy to discern where two species have common limits. Dashed lines indicate uncertainty, usually explained in the text.

netic, biochemical, and other more modern tests, it still seems legitimate to construct hypotheses concerning what has happened to *Atelopus* phylogeny in Ecuador. The potential absurdity and essential sterility of such hypotheses can only become evident after considerable research on the taxa concerned, research which I do not anticipate being done for many years—and which might even verify my guesses here.

In any event, the evidence derived from an examination of the distribution and morphology of the two groups of species indicates the direction that evolution has taken. With regard to distribution, the taxa of the *longirostris* group are almost entirely low altitude species. The only exception may be *A. planispinus*, which is found on Mount Sumaco, which reaches an altitude of 3900 meters. The type locality for the species, at the foot of the mountain, is at 500 meters, and specimens in the American Museum of Natural History are recorded as coming from the top of Sumaco, which gives the species a possible altitudinal range of 500 to 3900 meters, a most unlikely situation. Since this taxon is part of the *longirostris* group, and since it has not been taken elsewhere in the Amazonian lowlands, as would be expected if it actually occurred at San José Nuevo (the modern name for San José de Moti, or Mote), I predict it will eventually be found to occupy the slopes of Sumaco at lower to intermediate altitudes (perhaps 1000 to 2000 meters) and probably on the eastern slope only (because of habitat change on the back or western side of the mountain). Other than *A. planispinus*, the taxa in the *longirostris* group do not reach altitudes above 2000 meters, and enjoy their greatest abundance below 1000 meters.

The taxa of the *ignescens* group, on the other hand, are almost all high altitude forms. The one exception, *A. mindoensis*, is an enigma. As I point out frequently in this paper, this taxon is intermediate between the two groups in many ways. For example, it tends to fall halfway between the groups in almost all of the analyses of proportional measurements. Leaving that species to one side, the remaining members of the *ignescens* group all show a common zoogeographic pattern. They are very restricted horizontally, and appear to be equally restricted vertically to a fairly narrow altitudinal band. They have not, and I believe they are unable to, spread widely on a horizontal plane,

although the horizontal distribution of each is certainly greater than my data show. The vertical restrictions are for the most part real, and I think the various taxa show sharp response to and are closely confined by the changing conditions which accompany increasing altitude. All of these species are living in a comparatively young area, geologically speaking. The surrounding lowlands are much older, and it seems plausible that the ancestral species in the genus *Atelopus* are the lowland taxa, and the highland taxa have been repeatedly derived from the lowland stocks. I would further suggest that each of the highland taxa (with the probable exception of *A. ignescens* and the possible exception of *A. bufoniformis*) is the product of a separate, successful invasion of the highlands by lowland stock. This, of course, means that the *ignescens* group is clearly not monophyletic, but simply represents a series of separately derived species all differentiating from the ancestral stock along similar morphological lines.

The morphology of the two groups of species tends to verify the hypothesis. The adaptive changes evolved in response to higher altitudes and colder temperature include shorter, more stocky bodies and a reduction of the limbs from long and slender to short and stout. This suggests, of course, the development of mechanisms to reduce total surface and concomitant heat loss. The highland species are much less likely than the lowland taxa to be found out and actively moving about except during breeding periods, when they become abundant.

While not as sharply distinctive between groups as the body and limb configuration, the thickening of the skin in the webbing between the digits, and the overall fleshiness of the highland species in general, may well be another modification toward heat conservation. It reaches maximum development in *A. bufoniformis*, the taxon which has both the maximum development of the characteristics discussed here and reaches, with *A. ignescens*, maximum altitudes.

McDiarmid (1971:58) has discussed the evolutionary relationships of *Atelopus* with other genera of the family Bufonidae, and demonstrated that the genus is quite advanced rather than primitive in a large number of its characteristics. He pointed out several phenomena concerning the genus *Ate-*

lopus that are of interest in understanding evolutionary events in Ecuador. He stated:

With the initial uplifts of the Andes in Peru and Ecuador in the Late Cretaceous . . . entire new areas became available to and were exploited by *Atelopus*. The ancestral stock probably came from southeastern portions of the Guiana shield where the more primitive *Atelopus flavescens* is found today. However, it is possible that *Atelopus* initially invaded the montane habitat in the southern Andes and moved north along their eastern slope. It appears also that the higher elevations have been invaded several times.

I would agree completely with the concept of multiple invasion of the higher elevations, but think it unlikely that there has been very much movement north along the eastern slope of the Andes from the south. The evidence presented above seems to indicate fairly strongly that lateral or horizontal movement is not a common phenomenon in Ecuador, probably as a consequence of multiple barriers. McDiarmid (1971:58) has himself provided an additional argument against horizontal movement, for he said:

The apparent close association of species of *Atelopus* with mountain streams has restricted species to particular drainage systems. The resulting isolation (drainage system and mountain top) probably accounts for the striking differences among many populations and probably has been an important factor contributing to speciation.

The only species of the *ignescens* group which has been able to break out of the limitations noted above for other species is *A. ignescens* itself. It has been a highly successful invader of the inter-Andean valleys in Ecuador, and its vertical range is such that the *nudos* or knots between the valleys are not a barrier to horizontal movement. The species ranges from the southernmost provinces in Ecuador well into Colombia, a horizontal range almost as great as that of any lowland species. Only *A. bufoniformis* shows greater differentiation than *A. ignescens* along the morphological sequences to high altitude adaptation, as can be seen in the graphs of proportional measurements. *A. ignescens* represents an explosive movement taking place, because its ancestral stock continued the upward expansion of its range until it spilled over the wall of the Andes, opening up the whole inter-Andean plateau to settlement.

The success and widespread distribution of *A. ignescens* leads one to a second look at the other members of its group. It is entirely possible that

they represent repeated successful invasions of the outer slopes by *A. ignescens*, adapting and differentiating in different areas. *A. ignescens* definitely occurs on the eastern slope within a few kilometers of *A. pachydermus*, and the relationship between them seems to be close. The same is true for *A. bomolochos*, which is equally close to *A. ignescens* both geographically and morphologically. Why, then, is it not possible that *A. ignescens* is the direct ancestor to these restricted populations?

Perhaps the strongest argument against this hypothetical ancestry is the fact that *A. ignescens* tends to maintain its specific identity throughout a considerable distance in the inter-Andean plateau. Although quite variable, and perhaps with recognizable subspecies in several places, it still remains one species throughout, in my estimation. It is uncertain how much contact there is between populations separated by *nudos*, but I suspect there is less contact between them than within such populations, certainly a situation to encourage local populational differentiation, if the species is plastic enough to respond. I suggest that *A. ignescens* is a species well advanced evolutionarily, and highly adapted to a very inhospitable environment, and therefore has comparatively little evolutionary potential. The likelihood of such a species invading a series of isolated drainages on both sides of the Andes of Ecuador and giving rise to such a large number of very distinct species as are found there seems very slight to me.

On the other hand, I must reverse that argument with regard to *A. bufoniformis*. This species has gone beyond *A. ignescens* in every one of the adaptive characteristics discussed here. It is clearly the terminal species in the differentiation sequence. It is difficult for me to visualize any other ancestor for this species than *A. ignescens*, and this causes some considerable discomfort. At one time I had thought *A. bufoniformis* to be an inhabitant of the high eastern slope, found slightly below the range of *A. ignescens*. But material in the UKMNH collections show it from 3400 meters, and well into the higher parts of the inter-Andean Plateau. It does not seem to occur in the inter-Andean valleys, although it has been found low enough on the outer slopes that altitude would not be a barrier. It appears to have been a comparatively recent derivative of *A. ignescens* stock, and is perhaps even more thoroughly adapted to the cold, wind-

swept, high altitude *paramo* than the parent stock. It is probably in the process of expanding its range at those high altitudes, but may face problems in the fact that the habitat it utilizes is not sufficiently continuous to permit it to reach all existent *paramo*.

Literature Cited

- Acosta Solís, M.
1944. *Nuevas Contribuciones al Conocimiento de la Provincia de Esmeraldas*. 606 pages. Quito: Editorial Ecuador.
- Andersson, Lars G.
1945. Batrachians from East Ecuador Collected 1937, 1938 by Wm. Clarke-MacIntyre and Rolf Blomberg. *Arkiv för Zoologi*, 37A (2):1-88.
- Boettger, O.
1892. *Katalog der Batrachier-Sammlung in Museum der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main*. 73 pages. Frankfurt a. M., Germany.
- Boulenger, George A.
1880. Reptiles et Batrachiens recueillis par M. Émile de Ville dans les Andes de l'Équateur. *Bulletin de la Société Zoologique de France*, 1880:41-48.
1882a. *Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum*. Second Edition, 495 pages, 30 plates. London: British Museum.
1882b. Account of the Reptiles and Batrachians Collected by Mr. Edward Whymper in Ecuador in 1879-80. *Annals and Magazines of Natural History*, series 5, 9:457-467.
1894. On the Genus *Phryniscus* of Wiegmann. *Annals and Magazine of Natural History*, series 6, 14:374-375.
1898. An Account of the Reptiles and Batrachians Collected by Mr. W. F. H. Rosenberg in Western Ecuador. *Proceedings of the Zoological Society of London*, 1898:107-126.
- Cochran, Doris M., and Coleman J. Goin
1970. Frogs of Colombia. *United States National Museum Bulletin*, 288:xii + 655 pages.
- Cope, Edward D.
1867. On the Families of Raniform Anura. *Journal of the Academy of Natural Sciences of Philadelphia*, series 2, 6:189-206.
1868. An Examination of the Reptilia and Batrachia Obtained by the Orton Expedition to Equador and the Upper Amazon, with Notes on other Species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 20:96-140.
- Cornalia, Emilio
1849. *Vertebratorum Synopsis in Museo Mediolanense Extantium quae per Novam Orbem Cajetanus Osculati Collegit Annis 1846-47-48. Museo Mediolanense, 1849:304-315.*
- Duellman, W. E., and J. D. Lynch
1969. Descriptions of *Atelopus* Tadpoles and Their Relevance to Atelopodid Classification. *Herpetologica*, 25:231-240.
- Dunn, Emmett R.
1931. New Frogs from Panama and Costa Rica. *Occasional Papers of the Boston Society of Natural History*, 5:385-401.
- Espada, Marcos Jimenez de la
1875. *Vertebrados del Viaje al Pacífico verificado de 1862 a 1865 por una Comisión de Naturalistas enviada por el Gobierno Español*. 208 pages, 6 plates. Batracios: Madrid.
- Guibe, Jean
1948. *Catalogue des Types d'Amphibiens du Muséum National d'Histoire Naturelle*. 71 pages. Paris: Imprimerie National.
- Günther, Albert
1858. *Catalogue of the Batrachia Salientia in the Collection of the British Museum*. 160 pages. London: British Museum.
1859. Second List of Cold-blooded Vertebrates Collected by Mr. Fraser in the Andes of Western Ecuador. *Proceedings of the Zoological Society of London*, 1859:402-420.
- McDiarmid, Roy W.
1971. Comparative Morphology and Evolution of Frogs of the Neotropical Genera *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella*. *Bulletin of the Los Angeles County Museum of Natural History, Science*, 12:1-66.
- Nieden, F.
1926. Amphibia. Anura II. Engystomatidae. *Das Tierreich*, 49:1-110.
- Noble, G. K.
1921. Five New Species of Salientia from South America. *American Museum Novitates*, 29:1-7.
- Orton, James
1871. Contributions to the Natural History of the Valley of Quito-II. Reptiles. *American Naturalist*, 5: 693.
- Parker, H. W.
1934. Reptiles and Amphibians from Southern Ecuador. *Annals and Magazine of Natural History*, series 10, 14:264-273.
1938. The Vertical Distribution of Some Reptiles and Amphibians in Southern Ecuador. *Annals and Magazine of Natural History*, series 11, 2:438-450.
- Peracca, M. G.
1904. Viaggio del Dr. Enrico Festa nell'Ecuador a regioni vicine. Rettili ed Anfibi. *Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino*, 19 (465):1-41.
- Rivero, Juan A.
1963. Five New Species of *Atelopus* from Colombia, with Notes on Other Forms from Colombia and Ecuador. *Caribbean Journal of Science*, 3 (2,3):103-124.
1965. Notes on the Andean Salientian (Amphibia) *Atelopus ignescens* (Cornalia). *Caribbean Journal of Science*, 5:137-139.

1968. More on the *Atelopus* (Amphibia, Salientia) from Western South America. *Caribbean Journal of Science*, 8:19-29.
1969. Nota sobre *Atelopus carinatus* Anudersson y *Atelopus palmatus* Andersson (Amphibia, Salientia). *Memorias de la Sociedad de Ciencias Naturales La Salle, Caracas*, 29 (83):142-145.
- Savage, Jay M.
1960. A Revision of the Ecuadorian Snakes of the Colubrid Genus *Atractus*. *Miscellaneous Publications of the Museum of Zoology University of Michigan*, 112:1-86.
- Schmidt, Oscar
1857. Diagnosen neuer Frösche des zoologischen Cabinets zu Krakau. *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften, Vienna*, 24:10-15.
1858. Deliciae Herpetologicae Musei Zoologici Cracoviensis. *Denkschriften der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften, Vienna*, 14:237-258.
- Taylor, Edward H.
1952. A Review of the Frogs and Toads of Costa Rica. *University of Kansas Science Bulletin*, 35:577-942.
- Thominot, Alexandre
1889. Observations sur quelques Reptiles et Batraciens de la Collection du Muséum d'Histoire Naturelle de Paris. *Bulletin de la Société Philomathique, Paris*, series 8, 1:21-30.
- Trueb, Linda
1971. Phylogenetic Relationships of Certain Neotropical Toads with the Description of a New Genus. *Los Angeles County Museum, Contributions to Science*, 216:1-40.
- Werner, Franz
1901. Ueber Reptilien und Batrachier aus Ecuador und NeuGuinea. *Verhandlungen der k. k. Zoologische-Botanische Gesellschaft im Wien*, 1901:593-614.

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