MISCELLANEOUS PUBLICATIONS MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 112

A Revision of the Ecuadorian Snakes of the Colubrid Genus *Atractus*

BY

JAY M. SAVAGE

Department of Biology University of Southern California

ANN ARBOR MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN MARCH 10, 1960

MISCELLANEOUS PUBLICATIONS MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN

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A REVISION OF THE ECUADORIAN SNAKES OF THE COLUBRID GENUS *ATRACTUS*

INTRODUCTION

THE Neotropical snakes of the genus *Atractus* comprise a series of closely related species that have differentiated into innumerable local populations. Unfortunately, the tendency among herpetologists has been to name as distinct species any population sample or single specimen differing slightly from previously described forms. Consequently nearly all the recognized species of *Atractus* are based upon small samples, usually one individual, without regard for intrapopulational or individual variation in supposedly distinguishing characteristics. The result of this tendency has been the description of approximately 80 species of *Atractus*. The large number of recognized forms and the lack of understanding concerning their limits have precluded any attempt to analyze the relationships within the genus. Because of these factors, the natural populations of *Atractus* remain ill-defined, confusion exists as to the significance of their systematic characters, and the phylogenetic pattern within the group is unknown.

The logical way to attack these problems in Atractus systematics would be through a revisional study of the entire genus. Such a study, however, would require many more specimens than presently available, and cannot be accomplished at this time. In view of this material limitation I have selected an alternate method of clarifying some of the intricacies of Atractus classification. My approach has been to prepare an account of the genus as it occurs within a given political region, the Republic of Ecuador, with the hope that the information so accumulated might have wider implications when applied to Atractus from other regions. Ecuador was chosen because excellent series of the genus from that country are in the American Museum of Natural History, the Escuela Politecnica Nacional, Ecuador, and the Museum of Zoology, University of Michigan. The choice has proven to be an opportune one in that the region under discussion is small enough so as not to support an unwieldy number of populations, but is varied enough in physiography and climate to provide ecologic conditions suitable for considerable local differentiation.

The basic aims of this report are: (1) to analyze the variation within Atractus populations in order to ascertain those characters of systematic significance, (2) to define the natural units within the genus as they occur in Ecuador, and (3) to determine the relationships between the recognized populations.

METHODS, MATERIALS, AND ACKNOWLEDGMENTS

The usual methods applied to the study of snake systematics have been employed in the preparation of this report. Standard procedures have been utilized for descriptions of variation in scutellation, dentition, hemipenes, and coloration. These methods are discussed under the appropriate heading in the section on Variation in Systematic Characters. Characteristics of the maxillary dentition and male genitalia are used for the first time in defining populations and elucidating relationships in the genus. Throughout the paper, where more than one specimen is at hand, counts and measurements are given as follows: 1-3 (2.5). In this style of notation the arithmetic mean is in parentheses preceded by the minimum and maximum of the variational range. The mean has been rounded off to the nearest half unit in all cases to ensure that no greater significance will be attributed to the data than is permissible with small and not necessarily random samples.

Mensurational data are presented in a separate section under each species account. This section is divided into two parts. First is given the variational range and mean, expressed in millimeters, for each measured character. These figures are followed by a section listing the variational range of each measurement as a percentage of standard length. The sexes are treated separately in both sections in order to emphasize the measurements indicative of sexual dimorphism. Measurements are given for the following: Standard length; distance from tip of snout to anal opening. Tail length; distance from anal opening to tip of tail. Head length; distance from tip of snout to posterior tip of longer parietal shield. Head width; greatest width of head.

In the preparation of this paper no reliance has been placed upon published information regarding the characteristics and distribution of the species of *Atractus*. The literature on the group is rampant with misidentifications and errors based on ignorance of the significant features of the genus. Frequently reports of named species from regions far distant from their type localities are accompanied by so little data that allocation to any nominal form is impossible. Because of this confusion only those species originally described from Ecuador or of which Ecuadorian material has actually been seen by me are included within the limits of this report. I have attempted to place properly all published records of *Atractus* from Ecuador, but such allocations must be considered tentative unless the specimens have passed through my hands or have been examined for me by other workers.

Since the present paper deals exclusively with Ecuadorian material, several species recognized by me may eventually prove to be synonymous with extra-limital forms. Other Ecuadorian populations probably will turn out to be subspecifically allied to one another or to non-Ecuadorian species. Available information does not permit adequate investigation of these possibilities and it seems best under the circumstances to regard each distinct form as a separate species.

This report is based upon the examination of approximately 220 specimens of Ecuadorian Atractus. In addition, pertinent data on about 30 examples of the genus from the Republic have been supplied by various colleagues. Material of 13 of the 16 species recognized as valid in this paper have been examined. Two of the species not seen by me, Atractus dunni Savage and Atractus modestus Boulenger, are known only from holotypes. The original descriptions and notes kindly provided by the curators of the collections containing the types of these forms have made it possible to compare them with other species. The type and only known specimen of a third form, Atractus microrhynchus (Cope), is lost, and the wholly inadequate original description is my only source of information. Also available for study have been examples of 20 additional species from non-Ecuadorian localities.

The project was undertaken at the suggestion of the late Emmett Reid Dunn, who was contemplating a similar study on the genus in Colombia. I am greatly indebted to him as well as to Helen Thompson Gaige, long associated with the Museum of Zoology, University of Michigan, who was interested in Ecuadorian *Atractus* and surrendered her prior claim so that I might prepare this report. Both have generously supplied me with notes, suggestions, and criticisms of this work.

Individuals and institutions who have added materially to the study through the loan of specimens and in other ways are: J. C. Battersby, British Museum (Natural History) (BM); Charles M. Bogert, Bessie Matalas Hecht, and Richard G. Zweifel, American Museum of Natural History (AM); James E. Böhlke and Janvier Hamill, Academy of Natural Sciences of Philadelphia (AP); Doris M. Cochran, United States National Museum (US); Jean Guibé, Museum National d'Histoire Naturelle, Paris (PM); Norman E. Hartweg, Museum of Zoology, University of Michigan (UM); Alan E. Leviton, George S. Myers, and Margaret H. Storey, Natural History Museum, Stanford University (SU); Arthur Loveridge, Benjamin Shreve, and Ernest E. Williams, Museum of Comparative Zoology, Harvard University (MC); Gustavo Orcés V., Escuela Politecnica Nacional, Ecuador (EP, OV); Dwight L. Ryerson, Pomona College; and the Revolving Research Fund of the American Society of Ichthyologists and Herpetologists, then under the chairmanship of Fred H. Stoye.

Finally, I wish to thank James A. Peters (JP), the leading authority on the herpetofauna of Ecuador, for reading over the manuscript and offering valuable suggestions.

The abbreviations in parentheses are used throughout the report to indicate the location of catalogued specimens.

Notes on the physiography and climate of Ecuador and data on certain specific collecting localities have been derived primarily from Shelford (1926: 662–674), Chapman (1926: 23–133, 703–722), Brown (1941: 809–851), and from information kindly provided by Gustavo Orcés V. and James A. Peters.

PHYSIOGRAPHY AND CLIMATE OF ECUADOR

The dominant physiographic feature of Ecuador is the high Andean Cordillera, maximum elevation approximately 21,000 feet (6400 meters), that extends along a north-south axis from Colombia to Perú and separates the western coastal lowlands from the eastern lowlands of the upper Amazon Basin. As a direct consequence of the influence of the Andes, Ecuador can be divided into six major physiographic regions.

THE COASTAL PLAINS.-This region is mostly below 1000 feet (300 I. meters) and is continuous with the humid coastal belt of Colombia to the north and the desert coastal region of Perú to the south. North of Guayaquil the coastal area is about 100 miles wide (160 kilometers), but it narrows abruptly south of this region to form a narrow band about 20 miles (32 kilometers) in width, and is uninterrupted to the Peruvian border. In extreme northwestern Ecuador the coastal plain narrows to between 40 and 50 miles (64-80 kilometers) in breadth. There is a definite north to south gradient in the climate of the western lowlands best exemplified by the changing vegetation. The northern coastal area is covered with a dense lush rain forest, continuous with the tropical coastal forests of Colombia and Panamá. At about the level of Bahia de Caráquez the coastal plains become drier and deciduous forest replaces the tropical evergreens, although the tropical forest extends farther south inland from the coast. The most westward projecting points of the northern coastal plain, Cabo San Lorenzo and Punta Santa Elena, are very arid in contrast to the forests immediately to the east. The Santa Elena plain to the west of Guayaquil is particularly dry and resembles quite closely the desertic areas of northern Perú. The regions immediately to the north and west of Guayaquil receive considerable rain and are a mixture of tropical forest, deciduous forest, and savanna depending upon local rainfall conditions. South of the estuary of the Río Guayas along the east shore of the Gulf of Guayaquil the coastal plain is covered by a savanna association of low scrub interspersed with grassland. There are, however, scattered islands of tropic or subtropic forest as far south as El Oro Province. The savanna is replaced in turn in extreme southern Ecuador by a desert association typical of the northern Peruvian coast.

II. WEST ANDEAN SLOPES.—The Andes rise abruptly from the low coastal plain at an elevation of about 1500 feet (450 meters) to form a rather steep western slope. The slope is covered for the most part at altitudes between 3000 and 9000 feet (900–2700 meters) by a rich montane forest. The forest varies markedly in altitudinal extent depending on local conditions of temperature and humidity. There is, however, a gradual increase in the elevation of the lower limit of this forest from north to south and a tendency for the woodland to occupy a rather narrow belt in southern Ecuador.

III. THE ANDEAN CORDILLERA.—The main ridge of the Andes of Ecuador is essentially a single range. Several river valleys or hoyos lie along the Andean axis and it is usual to refer to the major peaks to the east or west of this axis as forming the Cordillera Oriental and Cordillera Occidental, respectively. The temperate, subalpine, and alpine areas of the Andes all lie above 9000 feet (2700 meters) and are included in the present physiographic unit. However, within the limits of this region, up to 21,000 feet (6400 meters), there are a number of climatic zones. Since *Atractus* has not been taken above 9000 feet, these additional zones are not discussed.

IV. THE INTERANDEAN BASINS.-The river valleys or hoyos that tend to lie along the main axis of the Andes in Ecuador are frequently grouped together as the Interandean Plateau. They are, however, mostly disjunct from one another and form a series of separate mountain valleys almost completely surrounded by the Andes. The principal hoyos, arranged in order from north to south with an indication of their position in drainage systems, are: Ibarra (Pacific), Quito (Pacific), Latacunga-Riobamba (Amazon), Chimbo (Pacific), Alausí (Pacific), Cañar (Pacific), Cuenca (Amazon), Jubones (Pacific), Zaruma (Pacific), and Loja (Amazon). These valleys lie at altitudes between 7000 and 9000 feet (2100-2700 meters). The more northern hoyos support savanna or grassland communities, but the Hoyo de Cuenca and the Llanos of Jubones and Zaruma are desertic, and the Valle de Loja is semi-arid. The Andean slopes south of Loja are very arid. An additional feature of the hoyos is the rain shadow effect of the bordering Andes that curtails the precipitation in these valleys and all but eliminates it along the surrounding Andean slopes.

V. EASTERN ANDEAN SLOPES.—The eastern slope of the Andes rises from the upper Amazon Basin at about the 4000-foot (1200 meter) level. These slopes are covered with a dense montane forest in regions of adequate rainfall at elevations between 3000 and 9000 feet (900–2700 meters). There is a tendency for the forests to be replaced to a considerable extent by scrub at lower elevations in southern Ecuador.

VI. ORIENTE.-The upper Amazon Basin area of eastern Ecuador is

covered by the typical tropical forest communities found from Venezuela and Colombia south through Brazil, Ecuador, Perú, and Bolivia in the upper Amazon Valley.

GAZETTEER OF LOCALITIES

This section presents a list of the principal localities from which snakes of the genus *Atractus* have been taken in Ecuador. Information on these places has been obtained from numerous sources, including Chapman (1926) and Brown (1941). All localities have been checked against the *Mapa Geográfica del Ecuador, compilado por el Instituto Geográfica Militar de Ecuador* (edition of 1950). Exact location and altitudes are always based upon this map where there is a difference of opinion as to these data in other sources. Altitudes, except for well-known localities, are approximate and are rounded off to the nearest 100 feet or 50 meters.

Dr. Gustavo Orcés V. has gone over this entire list for errors of commission and omission and has offered invaluable aid in finding obscure localities. He and James A. Peters have further enhanced the usefulness of the gazetteer by contributing suggestive information concerning mislabeled or confusing specimens with presumably erroneous locality data. The provinces are shown in Figure 1.

Abitagua, Tungurahua Province. An eastward projecting cordillera of the eastern Andes, just north of the Pastaza Cañon, at about $1^{\circ} 10'$ S and $78^{\circ} 7'$ W, reaching altitudes of 10,000 feet (3050 meters). Material from this locality appears to have been taken in the foothill region of this ridge at elevations around 3900 feet (1300 meters).

Río Aguarico, Napo-Pastaza Province. A large tributary of the Río Napo which it enters at 0° 57' S and 75° 12' W, altitute about 1800 feet (550 meters).

Alausí, Chimborazo Province. A town in the interandean region at 2° 11' S and 78° 50' W, altitude about 8550 feet (2600 meters).

Arajuno, Napo-Pastaza Province. A village on the south bank of the Río Arajuno, a tributary of the upper Río Napo of east Ecuador, lying at $1^{\circ} 17'$ S and $77^{\circ} 47'$ W, altitude 2200 feet (650 meters).

Avila, Napo-Pastaza Province. A town in the Río Napo drainage of eastern Ecuador, at 0° 38' S and 77° 27' W, elevation 2000 feet (600 meters).

Banos, Tungurahua Province. A town on the south bank of the upper Río Pastaza of eastern Ecuador, lying at 1° 25' S and 78° 33' W, altitude 6200 feet (1900 meters).

Río Bobonaza, Napo-Pastaza Province. A northern tributary of the Río Pastaza of eastern Ecuador, enters the Pastaza at 2° 35′ S and 76° 40′ W, elevation at this point about 800 feet (250 meters).

Canelos, Napo-Pastaza Province. An east Ecuadorian village on the upper Río Bobonaza, at $1^{\circ} 36'$ S and $77^{\circ} 48'$ W, altitude 1700 feet (500 meters).

Chanala, Santiago-Zamora Province. An east Ecuadorian village near the upper Upano on the trail from Riobamba to Macas; lying at 2° 10' S and 78° 27' W, altitude 7600 feet (2450 meters). Sometimes spelled Chamala.

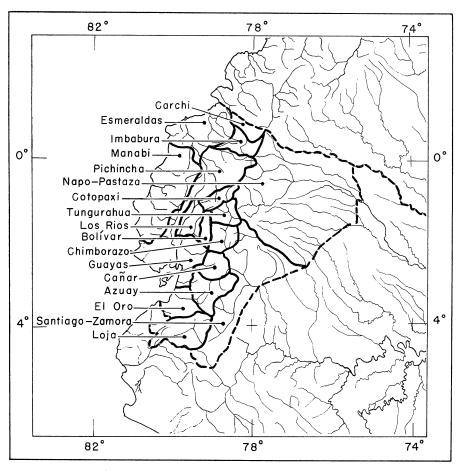


FIG. 1. Map of Ecuador indicating the Provinces.

Chicherota, Napo-Pastaza Province. An upper Amazonian Basin village near the point where the Río Bobonaza empties into the Río Pastaza, at about $2^{\circ} 32'$ S and $76^{\circ} 38'$ W, elevation 800 feet (250 meters).

Río Chiguancay, Chimborazo Province. A stream flowing into the Río Chanchán from the north between Huigra and Bucay on the west Andean slope; the Chanchán empties into the Río Guayas by the Río Chimbo. The mouth of the Chiguancay is at 2° 16' S and 79° 3'W, elevation 2600 feet (800 meters).

Chiguaza, Santiago-Zamora Province. A small village at the eastern base of the Andes, located at the mouth of the Río Chiguaza (Tuna-Chiguaza) where it empties into the Río Pastaza; lying at 1° 55' S and 77° 50' W, altitude 2000 feet (600 meters).

El Chiral, El Oro Province. A village on the west slope of the Andes on the trail between Santa Rosa and Portovelo, at 3° 32' S and 79° 12' W, elevation 5400 feet (1600 meters).

Chonta, El Oro Province. A village on the west slope of the Andes on the trail between Santa Rosa and Portovelo, at $3^{\circ} 35'$ S and $79^{\circ} 18'$ W, altitude about 4000 feet (1200 meters).

Río Coca, Napo-Pastaza Province. A tributary of the Río Napo which it enters at about 0° 27' S and 76° 58' W, altitude at this point 800 feet (250 meters).

Conambo, Napo-Pastaza Province. A village on the Río Conambo of the Río Tigre drainage of extreme east Ecuador, at 1° 52' S and 76° 48' W, elevation 1000 feet (300 meters).

Concepcion, Napo-Pastaza Province. A small village on the upper Río Napo at 0° 48' S and 77° 25' W, altitude 1200 feet (360 meters).

Río Cononaco, Napo-Pastaza Province. A major tributary of the Río Curaray of the upper Amazon drainage; joins the Curaray at approximately 1° 33′ S and 75° 40′ W, altitude 600 feet (200 meters).

Río Copataza, Napo-Pastaza Province. A tributary of the Río Pastaza into which it empties at 2° 05' S and 77° 27' W, altitude about 1500 feet (450 meters). This name is sometimes spelled Cupataza.

Río Corrientes, Napo-Pastaza Province. A tributary of the Río Tigre of northeastern Perú, lying between the Río Bobonaza and the Río Conambo; empties into the Río Tigre at 3° 45′ S and 74° 38′ W. All material from along this river in Ecuador is from below 2000 feet (600 meters) in elevation.

Río Cotopino, Napo-Pastaza Province. A tributary of the upper Río Napo of east Ecuador, enters the Napo at 0° 45' S and 77° 13' W, altitude at this point about 1000 feet (300 meters).

Cuenca, Azuay Province. A large town in the interandean region of central Ecuador at about 2° 53' S and 78° 58' W, altitude 8468 feet (2580 meters).

Gualaquiza, Santiago-Zamora Province. A village on the eastern slope of the Andes at 3° 22' S and 78° 33' W, altitude 3100 feet (950 meters).

Río Guataracu, Napo-Pastaza Province. A small stream tributary to the Río Suno of the upper Napo drainage of eastern Ecuador; empties into the Suno at 0° 42' S and 77° 20' W, elevation here about 1600 feet (500 meters).

Guayaquil, Guayas Province. A city about 45 miles north of the Golfo de Guayaquil on the Río Guayas of west Ecuador; lying at 2° 12' S and 79° 52' W, sea level.

Huigra, Chimborazo Province. A small town on the Río Chanchán at about 2° 17' S and 78° 59' W, elevation 4000 feet (1200 meters).

Intac, Imbabura Province. A westward projecting cordillera of the western Andes, lying at about 0° 15' N and 78° 30' W; this ridge reaches altitudes of 10,000 feet (3050 meters). Material in the British Museum recorded from this locality was apparently taken in the vicinity of a small farm (Tollo Intac) on the north slope of the cordillera along the south bank of the Río Llurimagua, altitude 1950 feet (600 meters), at 0° 20' N and 78° 44' W. This region is sometimes called Intag.

Río Lagatococha, Napo-Pastaza Province. A tributary of the Río Aguarico of eastern Ecuador, which it enters at $0^{\circ} 40'$ S and $75^{\circ} 17'$ W, altitude at this point 650 feet (200 meters).

Loja, Loja Province. A large town in the southern interandean region at about 4° 00' S and 79° 12' W, altitude 7300 feet (2200 meters).

Loreto, Napo-Pastaza Province. A village on the east bank of the Río Suno in the Río Napo drainage of east Ecuador, at 0° 38' S and 77° 20' W, altitude 1900 feet (600 meters).

Llanganate, Tungurahua Province. A prominent cordillera of the east Andes running from east to west at about 1° 15' S and 78° 15' W; continuous to the southeast with the Cordillera de Abitagua and attaining elevations in excess of 12000 feet (4000 meters).

Macas, Santiago-Zamora Province. A small town just west of the Río Upano of the Río Zamora system of east Ecuador, at 2° 17' S and 78° 18' W, altitude 3500 feet (1050 meters).

Macuma, Santiago-Zamora Province. A village of eastern Ecuador, at 2° 10' S and 77° 40' W, altitude 2000 feet (600 meters).

Río Mapoto, Tungurahua Province. A tributary of the upper Río Pastaza draining the southern slope of the Cordillera de Llanganate; enters the Pastaza at 1° 24′ S and 78° 16′ W, altitude at this point about 3900 feet (1200 meters).

Mendez, Santiago-Zamora Province. An east Ecuador village on the Río Paute, a tributary of the Río Upano of the Río Zamora system; lying at 2° 48' S and 78° 18' W, altitude 2300 feet (750 meters).

Mindo, Pichincha Province. A village on the western slopes of the Andes at 9° 02' S and 78° 50' W, altitude 4100 feet (1250 meters).

Montalvo, Napo-Pastaza Province. A village on the upper Río Bobonaza, at $2^{\circ} 04'$ S and $76^{\circ} 58'$ W, altitude 1100 feet (300 meters).

Normandia, Santiago-Zamora Province. An east Andean village near the upper Río Upano on the trail between Riobamba and Macas; lying at 2° 10' S and 78° 12' W, elevation 4300 feet (1300 meters).

Río Oglán, Napo-Pastaza Province. A tributary of the upper Río Curaray of east Ecuador, which it enters at 1° 19' S and 77° 35' W, altitude 2000 feet (600 meters).

Pallatanga, Chimborazo Province. A town on the west slope of the Andes, east of the Chimbo Valley at 2° 00' S and 78° 57' W, elevation 4900 feet (1500 meters). This locality has been made famous by the Buckley collections purchased for the British Museum (Natural History). Unfortunately it now appears that almost all the material reported from this locale is actually east Ecuadorian in character and it seems likely that through some error in labeling the locality became attached to Buckley material from Napo-Pastaza Province. This place has also been listed in the literature as Paitanga (apparently a result of phonetic transcription) and through an error on my part is listed as being in eastern Chimborazo Province in my previous report (Savage, 1955). I am indebted to Doctor James A. Peters for information leading to a clarification of the status of material recorded from Pallatanga or Paitanga. Also see Peters (1955:338).

Paramba, Imbabura Province. A farm on the south bank of the Río Mira of west Ecuador, at 0° 49' N and 78° 25' W, altitude 2500 feet (800 meters). Sometimes spelled Parumba.

Payamino, Napo-Pastaza Province. A village on the Río Payamino, a tributary of the Río Napo, at $0^{\circ} 30'$ S and $77^{\circ} 18'$ W, altitude 1000 feet (300 meters).

Río Pitzara, Pichincha Province. A tributary of the Río Guaillabamba of the Río Esmeraldas system of west Ecuador; enters the Guaillabamba at 0° 21' N and 79° 14' W, altitude at this point about 800 feet (250 meters).

Río Puncuno, Napo-Pastaza Province. A tributary of the upper Río Napo system of east Ecuador; enters the Río Suno at 0° 47' S and 77° 16' W, just before the Suno empties into the Napo; altitude at this point 1900 feet (600 meters).

Puyo, Napo-Pastaza Province. An east Ecuadorian village on the southwest bank of the Río Puyo at 1° 30' S and 78° 00' W, altitude 3000 feet (950 meters).

Riobamba, Chimborazo Province. A city on the large interandean plateau, lying at 1° 40′ S and 78° 38′ W, elevation 9000 feet (2700 meters).

Rutun Hill, Tungurahua Province. The northeast shoulder of the Volcán Tungurahua, lying just to the south of Baños on the trail to the top of Tungurahua; at 1° 26' S and 78° 24' W, reaches altitudes of nearly 10,000 feet (3000 meters).

San Francisco de Mapoto, Tungurahua Province. A farm on the north bank of the Río Pastaza, just east of the point where the Río Mapoto empties into the Pastaza; also called Mapoto or Quebrada de Mapoto; lying at 1° 24' S and 78° 16' W, altitude 3900 feet (1200 meters).

San Javier, Esmeraldas Province. A village on the north bank of the Río Cachabi, a tributary of the Río Santiago of west Ecuador, at 1° 04' N and 78° 47' W, elevation 160 feet (50 meters).

San José del Chimbo, Bolívar Province. A small west Andean town also called San José or Chimbo, lying at 1° 12' S and 79° 01' W, at an altitude of 8000 feet (2450 meters).

Santo Domingo de los Colorados, Pichincha Province. A village on the west slopes of the Andes at 0° 13' S and 79° 05' W, altitude 1800 feet (600 meters).

Sarayacu, Napo-Pastaza Province. A village on the north bank of the upper Río Bobonaza of east Ecuador, at 1° 45' S and 77° 29' W, altitude 1300 feet (400 meters).

Sucúa, Santiago-Zamora Province. A village west of the Río Upano, a tributary of the Río Zamora of east Ecuador, at 2° 24' S and 78° 10' W, altitude 2600 feet (800 meters).

Río Suno, Napo-Pastaza Province. A tributary of the upper Río Napo, which it enters at 0° 45' S and 77° 15' W, about 1000 feet (300 meters) altitude at this point.

Taisha, Santiago-Zamora Province. A village and airfield in the upper drainage of the Río Morona of the Amazon system, at 2° 23′ S and 77° 30′ W, elevation 1600 feet (500 meters).

Río Talín, Napo-Pastaza Province. A tributary of the Río Bobonaza of east Ecuador, enters the Bobonaza about 10 miles east of Puyo, altitude at this point 2100 feet (650 meters).

Turula (Tuvola), "Oriente." This locality is given for a number of east Ecuadorian species of amphibians and reptiles collected by Heinrich Feyer for the American Museum of Natural History. Dunn (1942:505) lists this place as Tuvola under eastern Ecuador and gives the elevation as 2800 feet (750 meters). I have been unable to find any place by this name in Ecuador and neither Dr. Orcés nor James A. Peters can determine its location.

Villano, Napo-Pastaza Province. A village on the Río Villano, a tributary of the upper Río Curaray, about 35 miles east of Puyo at 1° 30' S and 77° 28' W, altitude 1300 feet (400 meters).

Yunguilla, Tungurahua Province. A village on the north bank of the Pastaza Cañon, just east of the mouth of the Río Blanco, at 1° 24′ S and 78° 20′ W, altitude 5300 feet (1600 meters). Sometimes spelled Yungvilla or Yungilla.

Zamora, Santiago-Zamora Province. A village lying in the valley of the upper Río Zamora of east Ecuador, just to the east of the Cordillera de Zamora, at 4° 04' S and 78° 57' W, altitude 3300 feet (1000 meters).

Several series of snakes of the genus *Atractus* in the American Museum of Natural History, taken by the professional collector Heinrich Feyer, are cataloged from Riobamba, "Chamala" or Normandia. Most of this material is apparently from the immediate vicinity of Macas, Santiago-Zamora Province, which lies on the trail running from Riobamba through Chanala (Chamala) and Normandia to the Oriente. Riobamba lies in one of the arid and cold interandean hoyos at about 9000 feet (2700 meters) elevation. The two species of *Atractus, elaps* (Günther) and *major* Boulenger, supposedly from this place are known elsewhere only from material taken in the humid forests of eastern Ecuador at elevations below 3500 feet (1100 meters). Although Canala and Normandia are at slightly lower altitudes than Riobamba (between 4000 and 7000 feet; 1300–2500 meters), these places are also well above the known altitudinal ranges for *A. elaps* and *A. major*. Therefore, the original locality data on specimens of these species from the Amercian Museum collections are listed in this paper as from the Riobamba-Macas Trail, Chanala-Macas Trail, or Normandia-Macas Trail. All snakes in these samples were probably taken in the immediate vicinity of Macas, elevation 3500 feet (1100 meters).

A third species of the genus, *Atractus resplendens* Werner, is also represented in the Feyer material from these localities. Since the altitudinal range of the species is restricted to between 3500 and 6200 feet (1100–1900 meters) elsewhere in Ecuador, I have accepted the original locality data as being authentic for these specimens. The species is not represented in other collections from Riobamba and it seems likely that Feyer's examples are all from near Chanala and Normandia.

A considerable number of specimens of *Atractus*, as well as examples of other amphibians and reptiles, have been reported by workers at the British Museum (Natural History) from "West Ecuador," "West Andes of Ecuador," or "Andes of Ecuador." The material listed by these workers is without question of Ecuadorian origin. However, almost all of the specimens with these data represent species subsequently taken only in eastern Ecuador, usually in the lowlands. For this reason, unless there is additional evidence to the contrary which establishes the occurrence of particular species in the Andes or western Ecuador, I have placed no reliance on British Museum records from these generalized localities.

The status of two specimens of *Atractus* in the Buckley collections at the British Museum (Natural History), supposedly from Intac, Imbabura Province, is also confusing. The snakes appear to represent two species, *Atractus major* Boulenger and *Atractus occipitoalbus* (Jan), that are well represented by material from eastern Eucador. These examples differ slightly from samples of the species from across the Andes and may eventually prove to be from distinct populations restricted to the Pacific slopes. Until additional collecting is done near Intac, it seems best to regard these examples with suspicion and to assume tentatively that they are mislabeled material originating from east of the Andes. The chaos in locality data for Buckley's collections as noted under Pallatanga in the gazetteer and in the remarks on vague geographic data on other British Museum material makes this assumption most logical.

JAY M. SAVAGE

VARIATION IN SYSTEMATIC CHARACTERS

SCUTELLATION

HEAD SHIELDS.—Rostral (Fig. 2): This shield exhibits considerable intrapopulational variability in relative proportions and shape. However, the size of the rostral with relation to other head shields is a constant feature that serves to segregate the genus into two groups. The first group, represented in Ecuador by the red and black ringed *Atractus elaps* (Günther), has a large rostral, the scale being equal to or larger than a prefrontal. In all other Ecuadorian *Atractus* the rostral is rather small and never approaches a prefontal in size. In the species accounts, the *elaps*-type of rostral is referred to as "large," the second type as "small." The only other member of the genus known to have a large rostral is *Atractus latifrons* (Günther), a red and black ringed species closely allied to *A. elaps*. All other *Atractus* seen by me have a small rostral.

Internasals (Fig. 2): The size of the internasal shields appears to be directly correlated with the condition of the rostral. All Ecuadorian *Atractus*, except *elaps*, have internasals much less than half as large as a prefrontal. *A. elaps* has the internasals almost as large as the prefrontals. The former condition will hereafter be referred to as "small internasals" and the latter as "large internasals." Only *A. latifrons* among non-Ecuadorian species examined has large internasals.

Prefrontals (Fig. 2): The relative size of the prefrontals is positively correlated with the degree of rostral and internasal development. In A. *elaps* and A. *latifrons* the prefrontals are about as broad (measured along their margin of contact with the internasals) as long (measured along the median suture). In all other *Atractus* observed the prefrontals are always at least one and a half times as broad as long. The former condition is called "broad prefrontals" and the latter "long prefrontals" in the species accounts.

Frontals and Parietals: The relative proportions of these shields have been used by previous workers to distinguish between species of *Atractus*. I find in Ecuadorian members of the genus that the proportions of these two scales are subject to wide variation within local populations and that there are such extensive interpopulational overlaps between the various forms that the characters have little value. For these reasons the proportions of the frontal and parietals have not been employed for specific determinations in this study.

Postnasal and Loreal (Fig. 2): All known Atractus, except A. carrioni Parker, have the postnasal and loreal preventing any contact between the prefrontal and supralabial shields. The loreal is absent or represented by

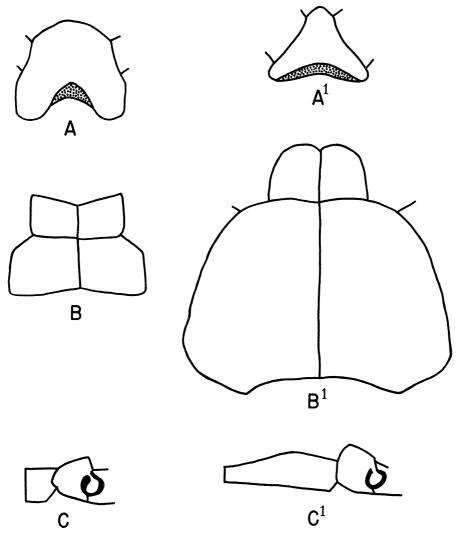


FIG. 2. Head scutellation in Ecuadorian species of *Atractus*. Series on right illustrates arrangement in *Badius* and *Trilineatus* groups; on left conditions in *Elaps* Group. A,A', rostral; B,B', internasals-prefrontals; C,C', loreal-postnasal area.

a small scale just anterior to the eye (referred to as a preocular in this paper) and the prefrontals meet the supralabials in *carrioni*. There are two types of postnasal-loreal relationships found in the remaining Ecuadorian *Atractus*. These appear to provide valid criteria for distinguishing between species in extralimital members of the genus as well. In the

species accounts, the loreal conditions are referred to as: (1) short loreal, in which the loreal is short, squarish, and about as long as the postnasal; and (2) long loreal, in which it is elongate and between two and four times as long as the postnasal. Most members of the genus have a long loreal, but A. elaps and A. latifrons have loreals of the short type.

Attractus modestus Boulenger, from western Ecuador, known from a single specimen, has a short loreal approaching the *elaps* condition. In all other features modestus appears to be similar to Atractus with long loreals and rather different from those, *elaps* and *latifrons*, with short loreals. It may be that the holotype of the species is anomalous in its loreal development. Rare examples from typically long loreal populations of non-Ecuadorian Atractus may have one or both of the loreals considerably reduced. It is thus probable that the type of A. modestus represents a rare occurrence and that additional material will probably establish that the population as a whole usually has long loreals.

The differences in the size of the loreals, prefrontals, internasals, and rostal are apparently the product of differences in relative head proportions. *A. elaps* and *A. latifrons* have rather broad heads and appear very blunt-snouted when compared with other forms. The sharp demarcation of the red and black ringed species from all other members of the genus in the nature of the cephalic scutellation (Fig. 2) is probably the result of the distinctive head shape.

Postoculars: In the past the number of postoculars has been emphasized as a method of diagnosing species of *Atractus*. Unfortunately, these scales are subject to a peculiar kind of variation that makes their use of dubious value.

Most individuals examined have either one or two postoculars on each side. Occasionally three postoculars are present or the postocular fuses with some other head shield, usually a supralabial or the parietal. The difficulty in employing the number of postoculars as a systematic character does not arise from these variations. It stems from the fact that in one population the number of postoculars may be extremely constant, while in other populations the number may be variable. When large samples are available the relative proportions of one versus two postoculars in a population may have some significance, but utilization of this feature in small samples is hopeless. Variation in postoculars for Ecuadorian species of *Atractus* is shown in Table I. The number of postoculars is recorded for both sides of the head so that the total number of snakes examined is equal to one-half the number of postocular counts.

The differences in proportions of the specimens with one or two postoculars within a population sample is not readily explained. The

Cracica.	Num	Totals			
Species	0	1	2	3	Totals
carrioni		16			16
collaris			4		4
dunni			2		2
ecuadorensis			2		2
elaps		109	5		114
aigeae			14		14
lehmanni			12		12
<i>major</i>		1	123		124
microrhynchus		1	I		2
modestus			2		2
multicinctus			12		12
occidentalis			5	1	6
occipitoalbus		16	28		44
paucidens			4		4
resplendens	2	48	6		56
roulei		14			14
Totals	2	205	220	1	428

 TABLE I

 VARIATION IN NUMBER OF POSTOCULARS IN ECUADORIAN SPECIES OF Atractus

variation is not obviously a result of the influence of environmental factors. This is shown by the fact that in samples with a constancy of a particular postocular count the snakes may be from a single locality (for example in a series of *elaps* from Macas, Santiago-Zamora Province, all have one postocular) or from a wide range of habitats (A. major, from almost all Ecuadorian localities, has two postoculars). On the other hand a sample of Atractus occipitoalbus (Jan) from Macas exhibits almost a 1:1 ratio between two postoculars and one postocular. In each instance ecologic uniformity or variability does not seem to affect the number of postoculars is controlled by some genetic factor or factors, perhaps even a single gene, that has varying frequencies in the different populations.

The presence of two postoculars should probably be considered a primitive condition while one postocular seems to be produced through failure of one of the scales to develop or through fusion (failure of the suture to develop). Supralabials: These shields tend to have high frequency of a given number within a population. In Ecuadorian material there are usually six, seven, or eight upper labials. Usually, the third and fourth supralabials enter the orbit in individuals with six or seven labials and the fourth and fifth enter the orbit when there are eight supralabials. Caution must be exercised when using this feature if small samples are being studied. Frequently a form with seven or eight labials will have the number of supralabials increased or decreased in as many as 25 per cent of the individuals. Insofar as I know there is no variation in species with six labials, although an increase to seven is to be expected on occasion.

It is difficult to determine what number of supralabials is most primitive in the genus. If it is assumed that six is the least specialized count, seven labials would have been produced by a division of one of the large labials posterior to the eye. Species with eight supralabials could have arisen from forms with seven labials through division of one of the labials anterior to the eye. The rarity of species with eight labials in *Atractus*, and the fact that in one form with eight labials, in Ecuador, seven supralabials are quite common, suggests that seven supralabials are primitive to eight. If we assume that the seven-labial condition was primitive, types with six labials would have been produced through fusion of two labials posterior to the eye. Other characteristics support this latter concept and in Ecuador, at least, forms with six labials appear to be a specialized group.

Infralabials: These shields usually number six or seven, but may be as many as eight or as few as five. There are usually three or four infralabials in contact with the chin shield on each side. The last infralabial, as counted for this report, usually lies at the angle of the mouth and under the penultimate supralabial. The number of infralabials seems to be more variable than the supralabial count, but it still may constitute a fairly sound character for population recognition. The infralabial count has not been utilized previously in *Atractus* systematics.

SCALE Rows.—The number of dorsal scale rows is constant for each population. The scales are almost always in 17 or 15 rows. Occasionally the number may be reduced on the neck to 16 or 14. Throughout this report when the number of scale rows is mentioned it indicates that the scale formula is 17-17-17 or 15-15-15.

It is not likely that all populations with the same number of scale rows are closely related. The forms with 17 rows are probably more primitive than species with the 15 rows, the latter group being the result of independent derivations from several forms with 17 scale rows. Evidence supporting this view is derived from the wide geographic separation between seemingly similar *Atractus* with 15 scale rows and the fact that there are many more species with 17 scale rows. SEGMENTAL COUNTS.—In common with most burrowing snakes, the genus *Atractus* exhibits strong sexual dimorphism in the segmental scale counts. In all forms examined by me, including extralimital ones, the males average about 10 fewer ventrals and 10 more caudals than the females. Ignorance of this condition has caused many workers to describe the males and females of the same population as distinct species. If the sexes are taken separately the segmental counts are of great importance in delimiting populations.

Correlated with the differences in ventral and caudal counts are the absolute standard length and the relative tail length (Table II). The standard length attained by females is always greater than that for males

Species	Standard Length in Millimeters		Variation Limits in Tail Length as a Percentage of Standard Length				
-	Male Female		Male	Female			
carrioni	282	350	13–16	9.6-11			
collaris		107*		8.4*			
lunni		305		11			
ecuadorensis	198		24				
elaps	560	631	12-17	8.4-9.8			
gaigeae	255	312	12-13	8-8.3			
ehmanni	262	296	13	10			
najor	512	852	15-22	10-14			
nicrorhynchus	101**		17**				
nodestus	330		15				
multicinctus	300	354	15-16	10-12			
occidentalis	265	315	21	11			
occipitoalbus	269	298	10-14	3.8-8			
paucidens		320		13			
resplendens	337	372	10-12	5.5 - 8.2			
roulei	330	396	10-12	7.4-7.8			

TABLE II

MAXIMUM STANDARD LENGTHS AND RELATIVE TAIL LENGTHS IN THE TWO SEXES IN ECUADORIAN SPECIES OF *Atractus*

* Immature specimen. ** Sex unknown.

ber unknown.

of the same species. The males always have a somewhat longer tail than the females. These differences probably are related to the carrying of eggs by the female and the location of the intromittent organ in the tail of the male.

No other scale count or proportion with the possible exception of head width seems to be affected by sexual dimorphism.

The sex of specimens reported in the literature is frequently not recorded or is subject to doubt. In order to make possible comparison between such examples and properly describe material it has been expedient to use the sum of the ventrals plus the caudals as a character. There does not appear to be any significant sexual difference in this count and although it tends to obscure differences between short-bodied, longtailed species and long-bodied, short-tailed forms it can be used as an additional taxonomic aid.

DENTITION

Herpetologists working on Neotropical colubrids have usually placed considerable emphasis on the nature and number of maxillary teeth. It is, therefore, surprising that aside from records of tooth numbers in generic descriptions little attention has been given to this character in *Atractus*. In Ecuador the number of maxillary teeth is diagnostic of each population (Table III). Pterygoid, palatine, and mandibular teeth have not been counted, but they probably have somewhat similar patterns. It is obvious that an adequate study of dental variation throughout the genus would provide a better understanding of populational limits and possibly of relationships.

Species	Number of Teeth							
Species	5	6	7	8	9	10	11	- Totals
carrioni				4	2	<u>.</u>		6
collaris	1							1
ecuadorensis				1				1
elaps		1	16	35				52
gaigeae	6	1						7
lehmanni				1				1
major	1	36	13					50
modestus					1			1
multicinctus	3	2						5
occidentalis		1	1					2
occipitoalbus			15	1				16
paucidens	1?	1						2
resplendens			24					24
roulei						2	2	4
Totals	12	42	69	42	3	2	2	172

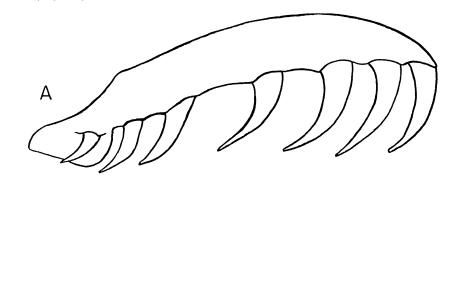
 TABLE III

 VARIATION IN NUMBER OF MAXILLARY TEETH IN ECUADORIAN SPECIES OF Atractus*

 Based on Examination of one Maxillary from each Specimen

* Maxillar tooth number unknown in dunni and microrhynchus.

Atractus elaps and A. latifrons differ slightly from the remainder of the genus in the structure of the maxillary teeth. In these two species the teeth are strongly compressed, elliptical in cross-section, rather short, and separated from one another by short interspaces (Fig. 3B). In all other Atractus examined, the maxillary teeth are not compressed, are essentially round in cross-section, and are separated from one another by larger interspaces (Fig. 3A).



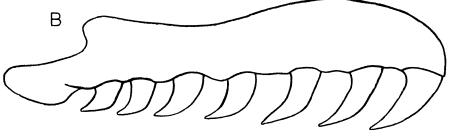


FIG. 3. Maxillary dentition in *Atractus*. A, maxilla of *A. carrioni* showing condition typical of *Badius* and *Trilineatus* groups; B, maxilla of *A. elaps* indicating characteristics of *Elaps* Group.

In recording the number of teeth each empty socket is counted as a tooth. The anterior maxillary tooth is located at the tip of the bone and is usually rather long and recurved. The last maxillary tooth is quite small and is frequently lost in dissection.

HEMIPENES

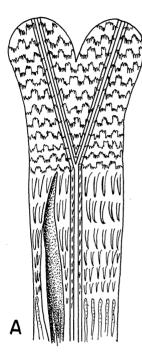
The Atractus of Ecuador fall into two well-defined subdivisions on the basis of hemipenial characters. All species agree in having each hemipenis bilobed at the tip, the sulcus spermaticus bifurcate, and a large basal naked pocket located lateral to the sulcus and sometimes reaching to the level of the sulcus division. The body of the hemipenis is divided into three distinct morphologic regions: (1) A series of short longitudinal plicae extend from the base of the organ to the level of the third to sixth caudal to form the basal plicate area. (2) A series of small to moderate sized spines cover the organ from the basal plicate area to the level of the sulcus division and form the *central spinous area* of the hemipenis. (3) The portion of the organ extending from the level of the sulcus division to the apex constitutes the *distal region*. The two groups of Ecuadorian *Atractus* differ markedly in details of the structure of the hemipenes, particularly in the distal region.

In the first group of species, characterized by a relatively unspecialized hemipenis, the entire organ, except for the short basal plicate area, is covered with small spines arranged in longitudinal rows; the spines are somewhat enlarged in most forms near the level of the sulcus division. This type of hemipenis is undifferentiated.

A more complex pattern is found in the second group. In these species the usual basal plicate area is present and the central spinous region is abruptly replaced at about the level of the sulcus division by a series of scalloped transverse flounces that extend to the apex of the organ. Each flounce bears a ridge of small papillae along its free margin. This organ is differentiated because of the sharp demarcation between the central spinous region and the distal flounced area. The differences between the two penial types are illustrated in Figure 4.

Although Atractus elaps has undifferentiated hemipenes, it differs from other species with similar genitalia in having the penial spines rather short and broad and of about equal length over the entire organs. In members of the Trilineatus Group, the spines in the region of the sulcus division are usually at least somewhat elongate and markedly larger than either the more proximal or distal spines. Most members of this section have the spines gradually decreasing in size toward the tip of the organs and these may sometimes be reduced to non-spiny papillae at the apex.

The descriptions of the hemipenes in the species accounts are from organs dissected *in situ*. A cut was made down the median lateral surface and the organ was then laid open. Whenever possible, several males were examined in an attempt to determine populational variation in this structure. The length of the organ, point of sulcus division, and degree of spinosity were recorded for each species. In some instances these features can be used to separate related forms.



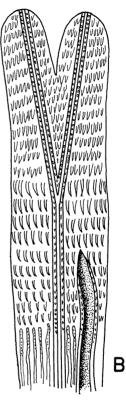


FIG. 4. Hemipenes of Ecuadorian species of Atractus. A, hemipenis of A. major, characteristic of Badius Group; B, Hemipenis of A. carrioni, typical of Elaps and Trilineatus groups.

COLORATION

Four basic color patterns are evident in *Atractus* from Ecuador: (1) blotches or bands on a lighter ground color; (2) longitudinal stripes on a lighter ground color; (3) a series of alternating rings of light (red and sometimes yellow) and dark (black) color; and (4) uniform dark brown, gray, or black.

The blotched or banded pattern is extremely variable in detail. Within a single population some individuals may be blotched, some banded, and others may have these dorsal markings modified into a checkerboard pattern. The dark markings are usually brown or black and show a wide range of shade, intensity, and extent. The pattern of striped individuals (Fig. 5) consists of a series of dark brown or black longitudinal stripes upon a lighter ground color. Differences in the number and arrangement of the stripes exhibit some intrapopulational variability, but the pattern appears to be characteristic of populational units. The basic pattern in the striped species is as follows: (1) a vertebral stripe, usually a single scale row in width; (2) a pair of dor-

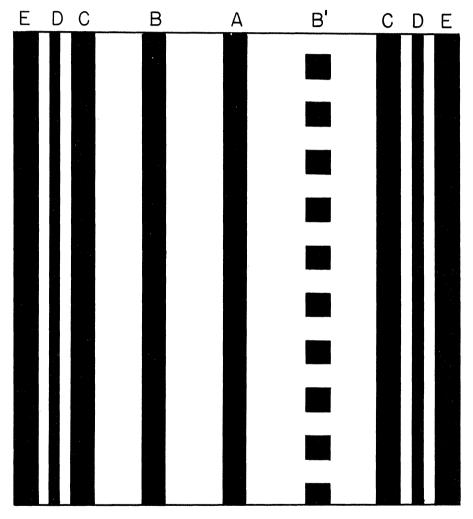


FIG. 5. Primitive dorsal color pattern of *Trilineatus* Group of *Atractus*. A, vertebral stripe; B, dorsolateral stripe; C, lateral stripe; D, lateroventral stripe; E, ventral stripe; B' indicates the dorsolateral blotches that are frequently present in some forms in place of the dorsolateral stripes.

solateral stripes occupying portions of two scale rows, but usually about a single scale row in width; (3) a pair of lateral stripes about a single row in width, but on portions of two scale rows; (4) a pair of narrow lateroventral stripes, between a quarter and a half a scale row in width on portions of two adjoining scale rows; and (5) a pair of ventral stripes about a single scale row wide, located on the lower portion of the first scale row and the tips of the ventrals. Frequently the dorsolateral stripes are represented by a series of regularly arranged squarish blotches or one to several of the stripes may be discontinuous.

The only ringed species in Ecuador, *Atractus elaps*, has a pattern consisting of a series of red, black, and sometimes white rings (probably yellow in life), that completely encircle the body.

A number of nominal forms have a uniform dorsal pattern, dark brown, gray, or black. In most cases the uniform pattern is characteristic of a given population, but in at least one Ecuadorian form, *A. occipitoalbus* (Jan), there are striped and uniform individuals from the same locality. Elsewhere in the genus there is evidence that the uniform pattern may occur as an occasional variant in typically blotched, banded, or striped populations. Very likely this pattern is the result of a melanistic tendency in which the underlying pattern is obscured by darker pigments. This concept is supported by the fact that in many essentially uniform individuals obscure dark stripes or blotches may be indicated under the superficial dark color.

A considerable number of blotched, banded, or striped species tend to have a light colored nuchal collar. The collar may form a complete, continuous light band across the neck, and usually includes portions of the parietal shields. Frequently, however, the light collar is more or less suffused with dark pigment even to the extent that it becomes completely obscured. In many individuals the dark suffusion is concentrated on the mid-line so that the light collar is separated into two discontinuous halves. In striped species of Ecuadorian *Atractus* the light nuchal collar is sharply set off from the dorsal coloration by a dark band that borders its posterior margin. This band is usually continuous with the longitudinal dorsal stripes of the body and tail. The condition of the nuchal collar is variable within material from the same locality in several species and does not appear to be of great systematic importance.

Most species of non-ringed *Atractus* have a considerable amount of dark pigment scattered over the ventral region. In some forms the entire belly except for the tips of the ventrals is dark, but usually this pigmentation consists of a series of fine punctations. Several forms, however, have some individuals with the color concentrated along the mid-line to form a definite mid-ventral stripe. The occurrence of this dark stripe does not appear to be a useful feature for taxonomic work. It may be present or absent in different specimens of the same species taken at the same place. The underside of the tail is often colored like the belly, but is usually entirely dark.

BODY PROPORTIONS

Mensurational data on standard length, tail length, head length, and head width are included in the species accounts primarily to complete the morphological description of each Ecuadorian form. Although the individual populations of *Atractus* have characteristic variational patterns for the recorded measurements, these features are not emphasized in distinguishing the recognized species. In the body of the report all measurements are presented as absolute values. Tail length, head length, and head width are also given as proportions of standard length to facilitate comparison of Ecuadorian *Atractus* with exotic forms by other workers.

The absolute standard length, its mean, and maximum are descriptive of each form (Table II). However, the considerable overlap in values between related species makes these statistics of relatively little use in diagnosis of the various populations. Marked sexual dimorphism is apparent in the standard length and is discussed above under the section on segmental counts.

The absolute tail length and the tail length as a proportion of standard length both show strong sexual dimorphism (Table II). Here again each population has a characteristic variational range, but there is so much overlap between related forms that few species can be distinguished on the basis of tail length statistics. Because this feature and standard length are subject to differential growth, juvenile individuals frequently have slightly different proportions when compared with adults of the same species and sex. The relative tail length appears to be directly correlated with the number of caudal scales, and the latter character is emphasized in this report in preference to the more variable and less definitive tail length to standard length ratios.

The head length and head width as proportions of the standard length also exhibit a distinctive variational range for each species of *Atractus*. Both ratios are subject to differential growth patterns and juvenile examples have markedly higher values or, more correctly, relatively longer and broader heads than do adults of the same species. The head width is most strongly affected by differences in growth rates and some sexual dimorphism in the head width to standard length proportion is indicated by my data. In general, males tend to have slightly higher head widthstandard length ratios than are found in females. However, there is extensive overlap between the sexes of the same species in these values and additional work is needed to verify the suggested sexual differences.

REVISION OF Atractus

SYSTEMATIC SECTION

GENUS Atractus WAGLER 1828

Type of genus, Atractus trilineatus Wagler, 1828, by monotypy.

Colubrid snakes with head not distinct from neck; upper surface of head with "normal" complement of head shields—a rostral, two internasals, two prefrontals, a frontal, two supraoculars, and two parietals. Nostril in suture between pre- and postnasal, closed by a prominent nasal valve. A single pair of enlarged chin shields. Pupil of eye round. Dorsal scales smooth, without apical pits, in 15 or 17 rows (rarely 14 or 16 on neck) throughout length of body. Anal plate entire; caudals divided. Maxillary teeth five to 13, almost equally spaced, last one or two teeth markedly shorter than the others; pterygoid and palatine toothed; mandibular teeth decreasing in length posteriorly. No hypapophyses on posterior dorsal vertebrae. Hemipenes bilobed at tips; sulcus spermaticus bifurcate; body of organ with well-developed spines; may be differentiated or not; never calyculate, although plicae and papillae may be present; a well-developed lateral naked pocket at base of organ.

SUMMARY OF COMMON CHARACTERS.—Except as indicated, all Ecuadorian *Atractus* share the following characteristics. Occasional aberrant specimens will not agree with all these generalizations. Rostral meets first supralabial, prenasal, and internasal. Internasals contact rostral, the nasals, the pre-frontals. Prefrontals roughly rectangular, in contact with internasal, postnasal, loreal, supraocular, and frontal, and extend to upper anterior margin of orbit. Supraoculars small, bordered by prefrontal, frontal, parietal, and postocular. Frontal roughly triangular, rather variable in relative proportions; usually about as broad as long or only a little longer than broad, and meeting the paired prefrontals, supraoculars, and parietals. Parietals rather elongate, anteriorly meeting a postocular, a supraocular, and the frontal, much longer than broad.

Nostrils between two scales; prenasals meet rostral, internasal, postnasal, and the first supralabial. Postnasal in contact with internasal, prenasal, two supralabials, and loreal. Loreal present and well developed, except in *Atractus carrioni*, separates prefrontal from supralabials; bordered by postnasal anteriorly, two to four supralabials below, and extends posteriorly to margin of orbit. No loreal in *A. carrioni*, although occasionally a small preocular scale present just anterior to eye; in this form prefrontal meets supralabials. No preoculars, except in *carrioni*, or suboculars; loreal and supralabials border eye anteriorly and below. Postocular separates anterior temporal, parietal, and one supralabial from orbit. Anterior temporal meets postocular and separates parietal from supralabials. Posterior upper temporal meets parietal, may be elongate or transversely divided, lower meets supralabial line. Two supralabials enter orbit. First pair of infralabials separates mental from chin shields.

In the species accounts, no character mentioned in the generic definition or the outline of common characters is reiterated. The features emphasized in the specific diagnoses are not repeated in the body of the species description.

STATUS OF THE GENUS, WITH REMARKS ON QUESTIONABLE FORMS .-Atractus appears to be closely allied with the genus Geophis Wagler, 1830, of México, Central America, and northern South America. The two genera differ in the structure of the hemipenes. In Geophis these organs are not bilobed, they do not have the lateral naked pocket, and they frequently have calyculate tips. No other characteristic will consistently separate the two groups, although Boulenger (1894) and others have attempted to segregate Atractus from Geophis on the basis of temporal formulae (1+2)in the former versus 0+2 in the latter). As shown elsewhere in this paper the temporal formulae are variable within local populations of Atractus and cannot be used to distinguish the genus from Geophis. In some instances specimens have the temporal formula of Atractus on one side of the head and that of Geophis on the other, according to Boulenger's criterion. Positive identification of members of the Atractus-Geophis stock, thus, rests upon examination of the characteristics of the male genitalia. This, however, does not create much of a problem in actual practice because the two genera have mutually exclusive ranges except in Panamá and Colombia. Generic identification in the area of overlap is relatively simple since all Geophis known from this region have two pairs of chin shields. Members of the genus Atractus always have a single pair of chin shields.

The genus Geophis as presently understood consists of a series of welldistinguished species groups that make for rather broad generic limits. Within the genus there are different forms having either one or two pairs of chin shields, the anterior temporal present or absent, the internasals present or absent, the supraoculars present or absent, and the dorsal scales smooth or keeled. This great diversity in structure suggests that the genus may not constitute a completely natural unit and this possibility may explain the difficulty of separating Atractus from Geophis. Unfortunately, the material available to me does not permit investigation of this problem in Geophis systematics. Additional work along this line is obviously necessary before the position of Atractus and its relationships to other Neotropical colubrids can be understood.

Several species of *Atractus* and *Geophis* have in the past been incorrectly placed as to genus. This seems an opportune time to examine their status.

REVISION OF Atractus

It has been usual to refer four South American species to the genus Geophis. These are Geophis diplozeugus Schmidt and Walker (1943); Geophis nigroalbus Boulenger; Rhabdosoma pöppigi Jan; and Geophis ruthveni Werner. The names diplozeugus and pöppigi are apparently based upon Peruvian and Brasilian examples of Atractus elaps (Günther, 1858), in which the anterior temporals are fused with a supralabial. Specimens with this condition occur occasionally throughout the range of A. elaps. Reference of these examples to Geophis is based upon the temporal formula, a character of little significance for generic determination in these snakes. The types of both diplozeugus and pöppigi are ringed specimens with a single pair of chin shields and the other characters of Atractus. Geophis nigroalbus appears to be properly placed generically. The species is known from two localities in Colombia, Pavas, Valle de Cauca, and Landázuri, Santander.

Werner's (1925) species, Geophis ruthveni, supposedly from Sarapiquí, Brazil, is more difficult to allocate. E. R. Dunn (in litt.) suggested that the type locality may be in error as Sarapiquí is a well-known river and district in Costa Rica, but the name is not given on any map or in any gazetteer of Brazil. Dunn further pointed out that ruthveni is strikingly similar to Geophis hoffmanni Peters, of Costa Rica and Panamá. If Werner's notorious ability to confuse locality data is taken into account it seems that Dunn's conclusions are most logical. Until information to the contrary is produced I follow Dunn in regarding Geophis ruthveni as a non-South American species.

Aside from the Central American and Mexican Geophis (isthmicus Boulenger; latifrontalis Garman; and longiceps Cope) placed by Boulenger (1894: 301) in Atractus, only two other species seem to have been included in the genus in error. Both of these are from South America, the first being Boulenger's (1894: 304) Atractus vittatus (type locality, Caracas, Distrito Federal, Venezuela). The type and only known specimen has two pairs of chin shields, three supralabials enter the orbit, and the temporals, 1+1; it obviously cannot be placed in Atractus. My knowledge of the genus Geophis does not permit me definitely to refer this form to that genus. Significantly, the only species unequivocally belonging to the genus Geophis in South America, G. nigroalbus, differs markedly from vittatus. It is not impossible, however, that Geophis occurs in Venezuela, although the relationships of vittatus may lie elsewhere. Tentatively, the species may be placed in Geophis with considerable doubt.

Atractus trihedrurus Amaral (1926, type locality, São Bento, Estado do Santa Catarina, Brazil) has two pairs of chin shields and does not appear to be an Atractus. The temporal character (formula 1+2 in the type and

only known example) and the wide geographic separation from *Geophis* makes inclusion in that genus undesirable. The generic status of this species must be considered uncertain until the type is re-examined.

It is obvious from the foregoing remarks that only a single *Geophis* of certain generic position occurs in South America. Except for the *Atractus* from the Colombian habitat of *Geophis nigroalbus* only two Panamanian forms, *Atractus clarki* Dunn and Bailey, and an undescribed population allied to *Atractus crassicaudatus* C. Duméril, Bibron, and A. Duméril, occur in territory occupied by *Geophis*.

Rhabdosoma fuliginosa Hallowell, from Venezuela, is placed in the genus Atractus in a manuscript by E. R. Dunn. Examination of the holotype (AP 3333) confirms this allocation.

Calamaria favae de Filippi (1840: 16) has frequently been placed with Atractus although the type is from an unknown source. The original description is not adequate to make generic or specific allocation possible at this time. Under these circumstances and until the type specimen is re-examined this name is best regarded as a nomen dubium.

SPECIES ACCOUNTS Atractus carrioni Parker

Atractus carrioni Parker (1930: 208, 1 fig., views of dorsal and lateral areas of head; type locality, Loja, Loja Province, Ecuador); Parker (1932: 23; material from type locality).

DIAGNOSIS.—An Atractus unique within the genus in having no loreal shield. Readily distinguished by the following combination of characteristics: (1) 15 scale rows; (2) no loreal, although a small preocular sometimes present; (3) maxillary teeth eight or nine; (4) ventrals in males, 145–149 (146), in females, 152–159 (155); and (5) dorsal coloration essentially uniform dark gray or brown.

LEPIDOSIS.—Rostral small. Internasals small. Prefrontals long. If a small preocular is present it may be in contact with a supraocular or a supralabial or it may be separated from both of them. One postocular. Temporals 1+1, rarely 1+2; anterior temporal rarely partially fused with parietal. Supralabials six, third and fourth enter orbit. Infralabials four (16 per cent) or five (84 per cent), usually four, occasionally three meeting each chin shield. Caudals in males, 29–34 (31), in females, 21–27 (23); ventrals plus caudals, 174–179 (176.5).

HEMIPENES.—Each organ covered with spines except for basal plicate region. Spines very large in region of sulcus division, rapidly grading into shorter spines and papillae that cover tip of organ. Basal plicae small, short, and naked. Lateral pocket opposite sulcus spermaticus naked, small, reaching to level of fourth or fifth caudal. Sulcus divided at level of eighth caudal. Hemipenes reach to level of 12th caudal.

COLORATION.—Dark brown or gray above, with each scale usually heavily punctated with light pigment, edges of scales dark. Top of head dark brown or gray, with some light punctations usually present. Side of head dark, but supralabials with considerable light color especially along lower margins. Throat and chin range from almost immaculate cream to cream with heavy punctations of brown, especially on mental, infralabials, and chin shields. Belly heavily pigmented with dark brown or gray. In some examples pigment tends to be restricted to mid-line, but in others entire ventral

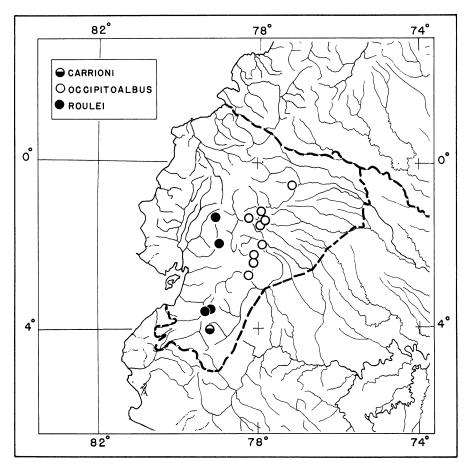


FIG. 6...Geographic distribution of those Ecuadorian species of the *Trilineatus* Group having 15 dorsal scale rows.

surface dark except for some light areas on tips of ventrals. Anal plate and underside of tail light with dark spotting to almost solid brown or gray with a few light punctations.

MEASUREMENTS.—Measurements are available from a sample of five males and three females having a standard length of 135–350 (250.5). Males: standard length, 135–282 (216); tail length, 18–38 (28.5); head length, 7–10 (8.5); head width 5–7 (6). Females: standard length, 260–350 (307.5); tail length, 25–39 (32); head length, 10–11 (11); head width, 7–7.5 (7.5). These measurements expressed as percentages of standard length have the following variational limits: Males: tail length, 13–16; head length, 3.5–5.2; head width, 2.4–3.7. Females: tail length, 9.6–11; head length, 3.2–3.8; head width, 2.2–2.7. The wide variation in head dimensions in males of this sample results from the inclusion of two young males, 135 and 152 mm. in standard length.

REMARKS.—Atractus carrioni is extremely close to Atractus roulei of southwestern Ecuador in all significant features. The two species differ primarily in the presence in roulei and absence in carrioni of the loreal shield. For full discussion of possible relationships to other species of Atractus see the description of A. roulei and the phylogenetic section at the end of this paper.

DISTRIBUTION.—This species is known only from the immediate vicinity of Loja, Loja Province (Fig. 6). All examples examined are from around 7000 feet (2100 meters). James A. Peters informs me that his material was collected along a wet slope watered by springs and several streams.

MATERIAL EXAMINED.—Loja: Loja (MC 31579, 28250); near Loja (US 98926); 1–2 miles (2–3 kilometers) E of Loja (JP 2490, JP 2557–60).

Atractus collaris Peracca

Atractus collaris Peracca (1897: 4, 1 fig.; type locality, Río Cononaco, Napo-Pastaza Province, Ecuador); Savage (1955. 14; record for Perú).

DIAGNOSIS.—A form obviously allied to A. gaigeae of Ecuador and A. bocourti of northeastern Perú, but distinct from them in both coloration and scutellation. Distinguished from all members of the genus known from Ecuador in: (1) 17 scale rows; (2) long loreal; (3) five maxillary teeth; (4) ventrals in male holotype 163, in female 175; and (5) pattern of six longitudinal dark stripes and a paired series of dorsolateral blotches.

LEPIDOSIS.—Rostral small. Internasals small. Prefrontals long. Postoculars two. Supralabials seven or eight, third and fourth enter orbit. Infralabials six, three meeting each chin shield. Caudals in male, 31; in female, 21; ventrals plus caudals, 194–196 (195). HEMIPENES.—These organs are not known for this species, but in view of the great similarity with *A. gaigeae* in other characteristics it can be predicted that *A. collaris* will prove to have hemipenes of the *trilineatus* type.

COLORATION.-Dorsal ground color light brown upon which are imposed six dark longitudinal stripes and a paired series of small dark blotches; a pair of lateral stripes on most of third and a portion of second scale rows; a pair of very narrow lateroventral stripes on upper margin of first and lower margin of second scale rows; a pair of broad ventral stripes on upper edges of ventrals and lower part of first scale rows; a paired series of regular dark dorsolateral blotches occupy portions of the sixth, seventh, and eighth scale rows. Blotches about two scales in total area, but on three or four scales. No vertebral stripe. Dark postnuchal area on neck prominent and demarcating posterior extent of light nuchal collar, continuous with lateral stripes. Nuchal collar reaches to posteriolateral border of parietals, its two arms completely separated from one another on mid-line by dark pigment. Top of head dark except for large light spots on prefrontals and internasals. Side of head dark brown with extensive light areas on supralabials. Throat and chin light, except for some brown markings on mental, infralabials, and chin shields. Belly, anal plate, and underside of tail immaculate, probably red in life.

MEASUREMENTS.—The single female example seen by me has a standard length of 107; tail length, 9; head length, 5; head width, 3. These measurements expressed as percentages of standard length are: tail length, 8.4; head length, 4.7; head width, 2.8.

REMARKS.—Atractus collaris appears to be intermediate in characteristics between A. gaigeae Savage of eastern Ecuador, and A. bocourti Boulenger, of eastern Perú (Table IV). Additional material will doubtless prove that the three populations are conspecific. However, in view of the lack of evidence regarding the status of other Amazonian populations that may belong to this same series of subspecies, I prefer to retain a binomial designation for each form.

Several specimens from northeastern Perú suggest intergradation between *collaris* and *bocourti*. Final evaluation of this situation must await study of more extensive material of both forms and determination of the characteristics of *Atractus* populations at the two type localities, Acomayo, Departmento de Huanuco, Perú, for *bocourti*, and the Río Cononaco, Napo-Pastaza Province, Ecuador, for *collaris*.

DISTRIBUTION.-Known only from extreme eastern Ecuador (Fig. 7) and northeastern Perú at elevations of 300 to 600 feet (100-200 meters).

MATERIAL EXAMINED.-Perú: Departmento de Loreto; Pébas (SU 12482).

JAY M. SAVAGE

Species	Ventrals		Ventrals	Color Pattern
	Males	Females	Plus Caudals	
bocourti	165	175	200	A series of more or less regularly arranged short dark lines or blotches. No continuous longitudinal stripes on dorsum.
collaris	163	175	194–196	Six continuous longitudinal dark stripes and a paired series of regular- ly arranged dark dorsolateral blotch- es; no vertebral dark stripe.
gaigeae	187–198	207–213	222-240	Seven longitudinal dark stripes and a paired series of dorsolateral dark blotches; a vertebral dark stripe.

 TABLE IV

 Distinguishing Characteristics of Three Species of Atractus

Atractus dunni Savage

Rhabdosoma maculatum Bocourt (1883: 539, Pl. 34, Fig. 2; type locality, Ecuador). Atractus badius (part) Boulenger (1894: 308; reference of Bocourt's female example to this species).

Atractus dunni Savage (1955: 14; type locality, Ecuador; PM 5986, Bocourt's female, designated lectotype of *Rhabdosoma maculatum* Bocourt, 1883, a secondary homonym of *Isocelis maculata* Günther, 1858; same specimen, holotype of *dunni*).

DIAGNOSIS.—A species closely related to *Atractus gaigeae*, but distinguished from that form and other Ecuadorian *Atractus* as follows: (1) 17 scale rows; (2) long loreal; (3) maxillary teeth not known, probably less than nine; (4) ventrals in female holotype, 144, probably about 10 fewer in males; and (5) pattern of five longitudinal dark stripes and two series of spots.

LEPIDOSIS.—Rostral small. Internasals small. Prefrontals long. Postoculars, two. Temporals 1+2. Supralabials, seven, third and fourth enter orbit. Infralabials, five, three meet each chin shield. Caudals, 20 in female type, probably about 30 in males; ventrals plus caudals, 164.

HEMIPENES.-No males known.

COLORATION.—Dorsal ground color brown with a vertebral dark stripe, two lateral stripes, a pair of ventral stripes, and a series of dorsolateral dark blotches on each side. Lateral stripes partially broken up into discrete spots. Light nuchal collar does not completely encircle neck, bordered posteriorly by dark area that is continuous with lateral stripes. Head mostly brown. Throat, belly, anal plate, and underside of tail light. MEASUREMENTS.—The single known example is a female, 305 in standard length, with a tail length of 34. The proportion of tail length to standard length is 11 per cent.

REMARKS.—This is a new name for *Rhabdosoma maculatum* Bocourt, which is preoccupied in *Atractus* by *Isocelis maculata* Günther. The description given above is derived from Bocourt's (1883) original account and plate and information kindly provided by M. Jean Guibé of the Paris Museum.

DISTRIBUTION.-The species is known from "Ecuador."

Atractus ecuadorensis Savage

Atractus ecuadorensis Savage (1955. 15; type locality, "Llangate area," Ecuador; probably refers to the Llanganate Range of eastern Tungurahua Province).

DIAGNOSIS.—A form similar to Atractus dunni and Atractus occidentalis of Ecuador, but differing from both in coloration and ventral counts. Distinct from all Ecuadorian Atractus in: (1) 17 scale rows; (2) long loreal; (3) maxillary teeth eight; (4) ventrals in male holotype, 144, probably about 10 higher in females; and (5) pattern composed of six longitudinal stripes that may be more or less interrupted.

LEPIDOSIS.—Rostral small. Internasals small. Prefrontals long. Postoculars two. Temporals 1 + 2. Supralabials seven, third and fourth enter orbit. Infralabials five, three meet each chin shield. Caudals, 41; ventrals plus caudals, 185.

HEMIPENES.—The tail of the type (CM 23529) is in poor condition and an accurate description of the penial structure is not possible. The organ appears to be essentially similar to that of *Atractus gaigeae* and extends to the level of the 12th caudal.

COLORATION.—Ground color a light brown upon which are superimposed a pair of dorsolateral dark stripes on the fifth and sixth or sixth and seventh scale rows; a pair of lateral stripes on the third and fourth scale rows; a third stripe on each side (lateroventral), most prominent anteriorly, running along the margins of the first and second scale rows; all stripes except the last frequently interrupted and discontinuous for several scales at a time. Head dark brown except for light areas on supralabials. Throat and chin light; mental, chin shields, and infralabials heavily mottled with brown. Belly and underside of tail light, with a sprinkling of brown marks that are most concentrated posteriorly.

MEASUREMENTS.-Data on the male holotype are as follows: standard length, 198; tail length, 48; head length, 8; head width, 4. These measure-

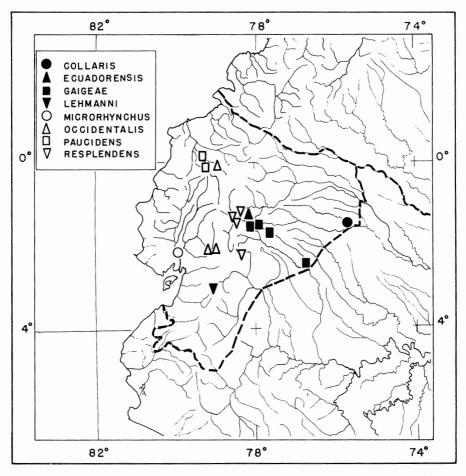


FIG. 7. Geographic distribution of those Ecuadorian species of the *Trilineatus* Group having 17 dorsal scale rows.

ments expressed as percentages of standard length are: tail length, 24; head length, 4; head width, 2.

REMARKS.—Atractus ecuadorensis resembles dunni and occidentalis more closely than any other members of the genus found in Ecuador. The differences between ecuadorensis and dunni in scutellation are relatively slight when due allowance is made for the sex of the types. However, the two forms are very different in coloration, ecuadorensis has no vertebral or ventral stripes, which are present in dunni. The differences between ecuadorensis and occidentalis of western Ecuador in lepidosis are slight, but occidentalis either has a vertebral stripe, or this stripe is absent and the other longitudinal stripes are broken up into short wavy lines. The relationships of *ecuadorensis* with *occidentalis* are probably more apparent than real. The former species is most likely a member of the *bocourti-collaris*gaigeae series found in the upper Amazon basin, while *occidentalis* may be most closely allied to similar forms in western Colombia.

DISTRIBUTION.-Known only from the type locality (Fig. 7); elevation unknown.

MATERIAL EXAMINED.—*Tungurahua*: Llangate area, probably Cordillera de Llanganate (CM 23529).

Atractus elaps (Günther)

Rhabdosoma elaps Günther (1858: 241; type locality, Guayaquil, Guayas Province, Ecuador, probably in error); Günther (1859: 411; list).

Rhabdosoma pöppigi Jan (1862: 11; type locality, Brazil); Jan and Sordelli (1865, Pl. 3, Fig. 4)

Rhabdosoma brevifrenum Jan (1862: 12; type locality, Brazil); Jan and Sordelli (1865, Pl. 4, Fig. 1).

Geophis elaps Günther (1868: 415; list).

Atractus elaps Boulenger (1894: 302; description, synonymy, list of specimens); Peracca (1897: 4; Río Cononaco, Napo-Pastaza Province, Ecuador); do Amaral (1929: 186; range).

Geophis poeppigii Boulenger (1894: 316; description, synonymy, based on Jan, 1862).

Atractus elaps tetrazonus do Amaral (1931: 87; type locality, Guaicaramo, E of Bogotá, Colombia).

Geophis diplozeugus Schmidt and Walker (1943:286; type locality Departamento de Madre de Dios, Perú).

DIAGNOSIS.—The striking coloration of this species readily distinguishes it from all other Ecuadorian *Atractus*. The diagnostic features of the population are: (1) 15 scale rows; (2) loreal short; (3) maxillary teeth seven or eight, rarely six; (4) ventrals in males, 135–154 (144); in females, 141–161 (152); and (5) body encircled by a series of red and black rings.

LEPIDOSIS.—Rostral large. Internasals large. Prefrontals broad. One (96 per cent) or two (4 per cent) postoculars. Temporals usually 1 + 2, sometimes 1 + 1 or 2 + 2, occasionally anterior temporal fused with fifth supralabial or parietal so that temporal formula is 0 + 2. Supralabials six, fourth and fifth enter orbit. Infralabials five (5 per cent), six (94 per cent) or seven (1 per cent), four or five meet each chin shield. Caudals in males, 28-37 (31); in females, 16-24 (20); ventrals plus caudals, 165-188 (174).

HEMIPENES.—Organ covered with spines for entire length except for basal plicate region; largest spines near base, spine size decreases from sulcus to tip. Basal plicae with small rows of spines. Lateral naked pocket extends to level of fifth caudal. Sulcus spermaticus divided at level of eighth caudal. Hemipenes undifferentiated, reach to level of 13th caudal. COLORATION.—Body encircled by a series of black and red rings; in some examples there is also a series of white rings; dorsally, the red and white rings may be suffused with black so that they are obscured; all rings clearly demarcated on belly. Head usually black above with a reddish collar usually crossing parietal region. Region below nostrils usually red with a dorsal extension upwards across snout. Throat usually light, often flecked with black. Red rings often appear as white in specimens that have been preserved for some time. White rings probably yellow in life, as indicated by freshly preserved material. Three different color phases are found within Ecuadorian samples of the species.

A. Dorsal pattern comprising a series of alternating red and black rings, with black rings very much broader in longitudinal extent. In some specimens black rings on posterior portion of body split by a single white (yellow) ring; white rings about as broad as red rings. Ventrally, black and red rings alternate with one another, with the two colors forming bands of about same longitudinal extent or black rings very slightly broader.

B. Dorsal pattern composed of a series of definite triads; each black ring split by two or three white (yellow) rings and widely separated from next black ring by a large red area. On belly, each red ring much broader than any of black rings, white (yellow) rings about same size as black rings.

C. Pattern appears as series of widely spaced black rings upon a red ground color; black rings very narrow, sometimes single, but frequently split by a single white (yellow) ring. Belly marked like back.

These three color patterns exhibit some geographic constancy in Ecuadorian material. Pattern A is found in specimens from the southeastern slope of the Andes. Patterns B and C are found in those from the north and central slopes of the eastern Andes and upper Amazon Basin region. Snakes with patterns B or C have been taken together at several localities in east Ecuador.

Because of the consistent distribution of the several color patterns in Ecuador some question arises as to whether more than one population of *elaps* ought to be accorded nomenclatural recognition. In all characters except coloration the two types of *elaps* are essentially identical. Furthermore, this is not strictly an Ecuadorian problem in that *A. elaps* occurs in the upper Amazon Basin from Colombia and Venezuela south through Ecuador and Brazil at least to Perú. The far reaching effect of a decision on the status of these color phases leads me to follow a conservative course until more material can be examined. For this reason all *elaps*-like *Atractus* are included under a single name without any attempt at subspecific differentiation.

MEASUREMENTS.—The standard length of the sample of 34 males and 23 females is 115–631 (359). Males: standard length, 152–560 (344.5); tail length, 22.5–88 (54); head length, 8–18 (11); head width 5–15 (8). Females: standard length, 134–631 (382); tail length, 12–58 (35.5); head length, 7–19 (13), head width, 5–15 (9). Variational range in these measurements as percentages of standard length are: Males: tail length, 12–17; head length, 2.8–3.8; head width, 2–3.8. Females: tail length, 8.4–9.8; head length, 2.8–3.7; head width, 1.7–2.8. Three juvenile males and two juvenile females all under 180 mm. in standard length were not included when calculating the proportions of head length and head width, because of the marked differential growth of the head.

REMARKS.—Günther (1858) based his name *elaps* on a specimen supposedly taken by Fraser at Guayaquil in the lowlands of western Ecuador. Subsequent collectors have failed to find a red and black ringed form of the genus west of the Andes. The holotype of *A. elaps* agrees in every respect with material from the eastern slopes of the Andes, so apparently the type locality is in error. Quite possibly, the specimen was shipped from Guayaquil and later labeled as coming from there, or some other mix-up in locality data occurred.

The synonymy of two names placed with this species requires further explanation. Both Rhabdosoma pöppigi and Geophis diplozeugus have usually been placed in the genus Geophis. As previously indicated in this report, all South American Geophis have two pairs of chin shields and unforked hemipenes. R. pöppigi and G. diplozeugus are based upon red and black ringed specimens with a single pair of chin shields. Apparently, the allocation of these forms to Geophis was made because the type specimens of both have the anterior temporal fused with an upper labial or parietal. This procedure follows the concept of Boulenger (1894) who separated the genera Atractus and Geophis on the basis of the temporal formulae (1+2) in the former versus 0+2 in the latter). As shown in the present paper, the condition of the temporals is variable within single specimens and the character is not indicative of natural groups. Examination of the original description of *pöppigi* and the holotype (CM 40251) of diplozeugus leaves no doubt that they are conspecific with Ecuadorian Atractus elaps.

The types of *pöppigi* (a female with 170 ventrals), *brevifrenum* (a female with 163 ventrals), and *diplozeugus* (holotype, a female with 169 ventrals, male paratype with 162 ventrals) all differ from Ecuadorian *elaps* in having more numerous ventrals. Material from northeastern Perú, Colombia, and Venezuela agrees with specimens from Ecuador in this count. Unfortunately, no large series were available to me from Brazil or central

Perú and it has not been possible to establish that the higher ventral counts are characteristic of a southern population of *elaps*. One other difficulty encountered in surveying this problem is that the color pattern of the type of *pöppigi* is very peculiar as figured by Jan and Sordelli (1865, Pl. 3, Fig. 4). In their example the red rings on the anterior portion of the body, at least, fail to encircle it completely and are suffused over dorsally by black pigment. If the differences in ventrals between the northern and southern examples of *elaps* prove to be consistent when more material is at hand, the name *pöppigi* would be the first available for the southern form. This usage would depend in part on whether the type of *pöppigi* was an occasional variant, in color pattern, within the southern population or whether it represents an additional local race not yet rediscovered.

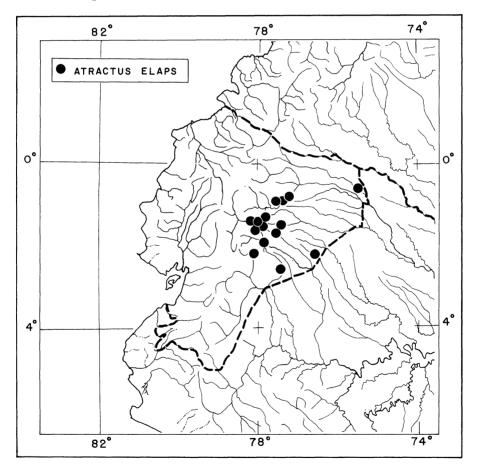


FIG. 8. Distributional records for Atractus elaps in Ecuador.

Atractus elaps is most closely allied to A. latifrons (Günther, 1868) of the Amazon forest area of Colombia, Brazil, and eastern Perú. A. latifrons exhibits a pattern dimorphism similar to that found in elaps, but in my material only patterns B and C occur. A. latifrons is distinguished from elaps in having 17 rows of dorsal scales and a more easterly range, but the two species are found together at some points in Colombia and Perú. Additional collecting may reveal that latifrons ranges into extreme eastern Ecuador.

DISTRIBUTION.—The upper Amazon basin from Venezuela and Colombia south through Ecuador (Fig. 8) and western Brazil into Perú and Bolivia; vertical range, 300 to 3500 feet (100–1100 meters).

MATERIAL EXAMINED.—*Napo-Pastaza*: Baños to Canelos (AM 35877); Canelos (AM 36031); Río Cotopino, 400 m. (UM 92023); Río Pastaza, 300 m. (UM 88999–89004); Sarayacu (AM 28802); Santiago-Zamora: no definite locality (UM 82883–84); Macas and vicinity (AM 28839–41, 28843–45, 28847, 28850–54, 35821–23); Riobamba-Macas Trail (AM 15222–28, 23305, 23312, 23320, 23322–23, 23353–54, 23361–62, 23364, 23368, 23373, 23376, 23394); Normandia-Macas Trail (AM 35910–17).

ADDITIONAL MATERIAL.—In the collections of the Escuela Politecnica Nacional are 51 specimens, not seen by me, from the following localities: Napo-Pastaza: Concepción; Canelos; Río Corrientes, near trail from Montalvo to Conambo; between Río Lagartococha and Río Aguarico, near Peruvian border; Loreto; Río Pucuno; between Puyo and Canelos; Sarayacu; lower Río Suno; Río Talín; Villano. Santigo-Zamora: Chiguaza; Taisha.

Atractus gaigeae Savage

Rhabdosoma maculatum (part) Bocourt (1883: 540, Pl. 35, Fig. 1; specimen from Ecuador, in Berlin Museum).

Atractus bocourti (part) Boulenger (1894: 306; Bocourt's specimen from Ecuador, in Berlin Museum); Boulenger (1896: 645; specimens from west Ecuador).

Atractus gaigeae Savage (1955: 12; type locality, Santiago-Zamora Province, Ecuador).

DIAGNOSIS.—A form most closely resembling A. collaris of Ecuador and Perú and, to a lesser extent, ecuadorensis, occidentalis, and dunni. Distinct from these forms and all other Ecuadorian Atractus in: (1) 17 scale rows; (2) loreal long; (3) teeth on maxillary five or six; (4) ventrals in males, 187–198 (191); in females, 207–213 (210); and (5) pattern of seven dark stripes and two rows of regularly arranged dark spots.

LEPIDOSIS.—Rostral small. Internasals small. Prefrontals long. Postoculars two. Temporals 1+2. Supralabials seven, third and fourth enter orbit. Infralabials six, usually three (rarely four), meeting a chin shield on each

side. Caudals in males, 35-39 (37); in females, 25-27 (26); ventrals plus caudals, 222-240 (230).

HEMIPENES.—Organ bilobed at tip, central and distal regions covered with spines; largest spines in region of sulcus division, decreasing in size toward base and apex. Small basal plicae mounted with minute hooked spines. Lateral fold or pocket well developed, extending from plicate area to level of fourth or fifth caudal. Pocket opposite the sulcus spermaticus, which is divided at level of seventh caudal. Hemipenes reach to level of 11th or 12th caudal.

COLORATION.-Dorsal ground color brown with seven dark longitudinal stripes imposed upon it as follows: a vertebral stripe, a single scale row wide; a pair of lateral stripes on lower half of third and upper half of second scale rows; a pair of irregular lateroventral stripes restricted to upper margin of first and lower margin of second scale rows; and a pair of ventral stripes on upper edges of ventrals and lower half of first scale row. A series of regularly arranged obscure dark dorsolateral blotches between vertebral and lateral stripes. A dark brown area on neck, continuous with lateral stripes, bordering posterior edge of light nuchal collar. Collar formed by light throat color which extends upward on neck as two narrow arms involving tips of parietals, but not meeting on the mid-line. Top of head dark except for light spots on anterior part of prefrontals, internasals, and in temporal region. Other head scales mainly brown, but lower portions of rostral, nasals, loreals and supralabials frequently light. Throat and chin light, with some brown markings on mental, chin shields, and infralabials. Belly immaculate, light (salmon in freshly preserved material). Underside of tail and anal plate light, former with a few median brown spots.

MEASUREMENTS.—The standard length of the sample of five males and two females is 197–312 (249). Males: standard length, 197–255 (228); tail length, 23.5–34 (29); head length 6–7.5 (6.5); head width, 3.5–5 (4). Females: standard length, 280–312 (296); tail length, 22–26 (24); head length, 6.5–7 (6.8); head width, 4–4.5 (4.2). Variation in measurements as percentages of standard length: Males: tail length, 12–13; head length, 2.6–3.1; head width, 1.5–1.9. Females: tail length, 8–8.3; head length, 2.2–2.3; head width, 1.3–1.6.

REMARKS.—As pointed out in my earlier paper (Savage, 1955: 13), this species was described by Bocourt (1883: 540) as part of his *Rhabdosoma* maculatum. His name was based upon a female Atractus in the Paris Museum (PM 5986) and a male in the Berlin Museum, both from "Ecuador."

When Boulenger (1894: 306, 308) placed maculatum in the genus Atractus, Bocourt's name became a secondary homonym of Isocelis maculata Günther, 1858, of Brazil (also an Atractus). To complicate matters further, Boulenger concluded that Bocourt's female is an example of the eastern South American species, Atractus badius (Schlegel), and included the male snake in the Berlin Museum in his new species Atractus bocourti (type locality, Acomayo, Departamento de Huanuco, Perú). Neither of these allocations was valid on the basis of coloration, longitudinal counts, or hemipenes, and in order to clarify the situation it was necessary to designate the Paris female as the lectotype of Rhabdosoma maculatum Bocourt and supply a new name, Atractus dunni, for this secondary homonym (see Savage, 1955: 14). The snake at the Berlin Museum is a male with 191 ventrals, 29 caudals, and a pattern as described above for gaigeae; unquestionably it is an example of that species.

On the basis of data kindly provided by J. C. Battersby of the British Museum (Natural History), two males in the collections of that institution appear referable to *A. gaigeae*. These specimens were placed under *Atractus bocourti* by Boulenger (1896: 645). One example (BM 80.12.12.8.13) from Canelos, Napo-Pastaza Province, has 190 ventrals and 36 caudals. The second specimen (BM 80.12.5.270) is listed from Paitanga, Ecuador, and has 189 ventrals and 35 caudals. The confusion surrounding the origin of material labeled as coming from Paitanga is discussed in the gazetteer under Pallatanga (p. 13).

DISTRIBUTION.-Restricted to the tropical forests of the upper Amazon basin of Ecuador (Fig. 7) between 600 and 2000 feet (200-600 meters).

MATERIAL EXAMINED.—Napo-Pastaza: between Baños and Canelos (AM 35891); headwaters of Río Bobonaza (OV 602; SU 15621); Canelos (SU 15619–20); Chicherota (EP 46; OV 726–27); Sarayacu (EP 48). Santiago-Zamora: no definite locality (UM 82887, holotype).

Atractus lehmanni Boettger

Atractus lehmanni Boettger (1898: 80; type locality, Cuenca, Azuay Province, Ecuador); do Amaral (1929: 187; list).

DIAGNOSIS.—A distinct member of the *Trilineatus* Group most obviously allied to *A. resplendens* and *A. dunni*, but differing from them in scutellation, dentition, and coloration. Distinct from other Ecuadorian *Atractus* in: (1) 17 scale rows; (2) long loreal; (3) maxillary teeth eight; (4) ventrals in males, 141–144 (143), in females, 148–153 (150); and (5) uniform dark brown dorsally.

LEPIDOSIS.-Rostral small. Internasals small. Prefrontals long. Two

postoculars. Temporals 1 + 2. Supralabials seven, third and fourth enter orbit. Infralabials six, four or five meeting each chin shield. Caudals in males, 25–28 (26), in females, 20–21 (20.6); ventrals plus caudals, 168–173 (169.5).

HEMIPENES.—Entire organ, except plicate region, covered with spines, largest ones near sulcus division, smallest at tip. Basal plicae short, surmounted with small spines. Lateral pocket extends to level of third or fourth caudal. Sulcus spermaticus divides at level of fifth caudal. Tip of organ extends to 11th caudal.

COLORATION.—Dorsally, appearing to be uniform dark brown; each scale, except those of first and second rows on each side, darkest on lower and posterior margins and marked with minute light punctations. An obscure vertebral stripe vaguely apparent. Lateroventral stripe of typical *trilineatus* complex pattern represented by dark upper edges of first scale row and dark centered scales of second scale row. Lower portions of scales in first row light. Light nuchal collar rather narrow, prominent, although somewhat suffused with dark pigment. Top of head mostly dark, but prefrontal-internasal region with some light areas. Supralabials and postnasals mainly dark, but lower portions light. Throat and chin light, but with large brown spots on infralabials, mental, and chin shields. Ventrals light, with irregular dark brown markings medially, giving impression of two light stripes running down each side of belly on tips of ventrals. Anal plate brown. Underside of tail light, with irregular brown mottling on median portion.

MEASUREMENTS.—Data are from the original description of the species and one male example examined by me. Standard length of two males and one female, 211–296 (256). Males: standard length, 211–262 (236.5); tail length, 26–33 (30); head length, 8; head width, 5. Females: standard length, 296; tail length, 32. Variation in measurements as percentages of standard length: Males: tail length, 13; head length, 3.8; head width, 2.4. Females: tail length, 10.

REMARKS.—The description of this form is based upon information provided by the original description and examination of one syntype (MC 33513).

A. lehmanni appears to be a melanistic member of the Trilineatus Group, somewhat intermediate in coloration between the typically striped forms A. gaigeae, A. collaris, A. ecuadorensis, and A. dunni, and the dark brown or black A. resplendens. Of the striped forms, A. dunni is similar to lehmanni in scutellation (ventrals in female type of dunni 144 versus 148-153 in lehmanni females). A. dunni is known only from "Ecuador" but is probably confined to the eastern Andes. A. lehmanni will probably prove to be closely allied to dunni when additional material of the latter is obtained. Ultimately these two nominal species may be shown to be conspecific, with striped or uniform color patterns occurring within a single population. A condition similar to this is already known for the east Ecuadorian species, A. occipitoalbus, with 15 scale rows.

DISTRIBUTION.—Known only from the hoyo of Cuenca, Azuay Province, a river valley draining into the Amazon basin (Fig. 7); elevation, about 8500 feet (2600 meters).

MATERIAL EXAMINED.-Azuay: Cuenca (MC 33513, a syntype).

Atractus major Boulenger

Rhabdosoma maculatum Günther (1859: 411; list).

Rhabdosoma badium (part) Jan (1862: 13); Jan and Sordelli (1865a; Pl. 1, Fig. 1).

- Atractus major Boulenger (1894: 307; type locality, Canelos, Napo-Pastaza Province, Ecuador); Peracca (1897a: 17; listed from Gualaquiza, Santiago-Zamora Province); do Amaral (1929: 187; range).
- Atractus badius Peracca (1897a: 14; specimen from Gualaquiza, Santiago-Zamora Province); Despax (1911: 29; notes on example from Gualaquiza, Santiago-Zamora Province).

DIAGNOSIS.—The largest Ecuadorian species, distinguished by the following combination of characteristics: (1) 17 scale rows; (2) long loreal; (3) maxillary teeth six or seven, very rarely five; (4) ventrals in males, 148–172 (159), in females, 157–181 (167); and (5) pattern or blotches or bands.

LEPIDOSIS.—Rostral small. Internasals small. Prefrontals long. Almost always two postoculars, rarely one. Supralabials seven (96 per cent) or eight (4 per cent), third and fourth or fourth and fifth enter in orbit. Infralabials six (91 per cent), seven (8 per cent), or eight (1 per cent), three or four infralabials meet each chin shield. Caudals in males, 31–49 (42), in females, 27–37 (32); ventrals plus caudals, 188–221 (200).

HEMIPENES.—Basal portion of organ with several longitudinal plicae, surmounted by series of small hooked spines. An elongate pocket extends apically from plicate area to about level of sulcus division. Each hemipenis differentiated, covered with large spines from level of fourth or fifth caudal to about level of sulcus division. At this point spines abruptly replaced by flounces that are covered with small papillae or spines. Flounced area extends to tip of organ. Sulcus spermaticus divides at eighth or ninth caudal. Tip of organ reaches to level of caudal 12 or 13.

COLORATION.—The basic color pattern of this species is a series of dark blotches superimposed upon a lighter ground color. This standard pattern is modified in various Ecuadorian examples into several distinctive variations.

A. The most common pattern in this form appears as a series of 20 to 25 dark brown blotches on a light brown ground color. Each blotch is usually surrounded by a light yellow border that separates the blotch from the background. The primary blotches are irregular in shape, position, and area, but frequently pass completely across the back and are broader than the light interspaces in longitudinal extent. A series of secondary blotches of the same color as the primaries occurs along the sides, usually alternating with the dorsal blotches and often fused with them. In specimens exhibiting this pattern there is no clearly indicated light nuchal area.

B. The pattern is essentially the same as in A, but there is usually no light margin around the dorsal blotches and the anterior spots tend to be fused to form two parallel elongate blotches on the neck. The dark blotches are usually narrower in longitudinal extent than the light interspaces. No light nuchal area.

C. The ground color is light brown with the dorsal blotches reduced to very narrow, irregular bands that are very much narrower than the light interspaces in longitudinal extent. Bands outlined by a clear light border. Numerous secondary blotches along sides which involve tips of ventrals. No light nuchal collar.

D. In this variant the dorsal dark blotches are expanded into rather definite regular cross-bands. These bands are about five or six scale rows in longitudinal extent and are separated from one another by light (yellow or white) interspaces of about two scale rows in breadth. Nuchal region light, but usually suffused with some darker pigment, especially dorsally.

E. Dorsal blotches regular and alternating with expanded lateral blotches to form a checkerboard pattern. Lateral blotches regular in size and shape, about same size as dorsal spots. Nuchal region light, but usually suffused with some dark pigment.

In all these color variants the head is dark brown above and on sides, although the upper lip is light. Chin, throat, belly, and underside of tail usually light, but almost always with heavy brown mottling or large dark spots. Sometimes undersides completely covered with brown pigment.

MEASUREMENTS.—The sample of 32 males and 24 females has a standard length of 120–852 (326). Males: standard length, 120–512 (301); tail length, 21–110 (58); head length, 7–19 (11); head width, 5–13 (7). Females: standard length, 140–852 (364); tail length, 18–89.5 (44); head length, 7–24.5 (18); head width, 5–18 (8.3).

In 26 males and 18 females exceeding 200 mm. in standard length the variation in proportion expressed as percentages of standard length are:

Males: tail length, 15–22; head length, 2.8–4.3; head width, 1.8–3.2. Females: tail length, 10–14; head length, 2.5–4.5; head width, 1.6–3. Six juvenile males and six juvenile females, all under 200 mm. in standard length, have the following proportions: Males: tail length, 15–20; head length, 3.6–5.2; head width, 3.1–4.0. Females: tail length, 12–14; head length, 4.1–5.7; head width, 3.2–3.6.

REMARKS.-Atractus major was originally described by Boulenger (1894) on the basis of three specimens listed by Fraser from west Ecuador (BM 60.6.16.61, 60.6.16.71, 60.6.16.72); one example supposedly taken by Buckley at Pallatanga (BM 80.12.5.272); another Buckley specimen labeled Intac (BM 78.1.25.50); and a specimen taken by Buckley at Canelos (BM 1946.9.7.27). The first three localities are in western Ecuador, but all material of this species seen by me is from east of the Andes. Data supplied through the kindness of J. C. Battersby leave no doubt that Boulenger's specimens, with the possible exception of the Intac example, are conspecific with east Ecuadorian snakes referred to Atractus major in this report. I have already discussed in an earlier section (see gazetteer) the confusion surrounding British Museum material labeled as coming from west Ecuador or Pallatanga. Many specimens collected by Fraser and Buckley that are labeled as being from west Ecuador have subsequently proven to be of species found only in the Oriente. Almost all British Museum material, supposed to be from Pallatanga, is representative of forms known only from eastern Ecuador. For these reasons Boulenger's specimens from these locales are presumed to be mislabeled.

The Intac specimen is more difficult to place. It is a female with eight maxillary teeth, 171 ventrals, 30 caudals, seven supralabials, and two postoculars. The only way in which this example differs from typical *major* seems to be in number of teeth and a unique color pattern, unlike any other *Atractus* seen in the course of this study. The ground color is light brown, and scattered upon it at irregular intervals are obscure dark brown spots each about the size of a single scale. Several of these spots may be lined up to form narrow cross-bands running obliquely across the back. The scales of the vertebral row are usually darker than the ground color giving the suggestion of a narrow vertebral stripe. The head is marked as in typical *major* with no light nuchal area. The underside corresponds in pattern to examples of *A. major* with a heavy suffusion of dark pigment and scattered dark blotches. The specimen is a large adult, 675 mm. in standard length.

The similarity of this snake to east Ecuadorian *major* in all features but dentition and coloration leads me to suggest that it be referred to that species. It seems extremely unlikely that the locality data are correct if the

specimen is *major*. It is possible, of course, that the Intac example is correctly labeled and represents a population of *Atractus* related to *major* and not subsequently taken in western Ecuador. If additional material of a *major*-like form with eight maxillary teeth and the peculiar coloration described above is discovered along the west Andean slope, the population should be awarded specific recognition. However, until such material is forthcoming it seems best to consider the Intac specimen as being mislabeled.

In order to prevent any further difficulty in the allocation of the name *Atractus major* Boulenger, the male specimen (BM 1946.9.7.27) from Canelos, Napo-Pastaza Province, Ecuador, is herewith designated the lectotype of the species. This example is a juvenile with 169 ventrals and 45 caudals. The standard length is 145 mm.; tail length, 25 mm.; head length, 9 mm.; and head width, 6 mm. The coloration is of type A as described above.

The material of this species at hand falls into two fairly distinct geographic groups on the basis of differences in ventral counts. Specimens from the slopes of the cordillera immediately to the north and west of the Pastaza Cañon (Abitagua, headwaters of the Río Arajuno, Mapoto, upper Río Pastaza, headwaters of the Río Talín and Villano) have more ventrals in both sexes than does material from farther south in the vicinity of Macas, Santiago-Zamora Province. Examples of the species from the lowlands of the Oriente are most like the Macas series in this character. A summary of the data for these areas is given in Table V.

The sample from the Pastaza Cañon region contains many individuals having a color pattern of type D as described above. The frequency of the occurrence of this pattern is very low in the remainder of my *major* material.

Considerable thought has been given to the problem of whether these two samples ought to be recognized as distinct forms. Because of the overlap in ventral counts between the two groups and the absence of any other distinguishing features I have retained them under a single name. Additional study of the variation within this widespread upper Amazonian species will probably result in the recognition of several subspecies. At that time it may seem advisable to segregate the two Ecuadorian populations. The ventral count for the male lectotype of *major* is 169, and this would seem to place it with the Pastaza Cañon series. The type locality, Canelos, is somewhat east and at a lower elevation than the localities from which my Pastaza material was taken.

In addition to the specimens seen by me there are two examples of *Atractus major* in the British Museum from 2 miles east of Loja, Loja Province, Ecuador. The male (BM 1933.6.24.98) has 161 ventrals and 43

Sample	N	Males	N	Females
Group I	<u>.</u>		·	· · · · · · · · · · · · · · · · · · ·
Pastaza Cañon	7	163–172 (166.5)	4	171–181 (177)
Group II				
Macas	18	148-159 (156)	17	159–173 (165)
Lowland Oriente		· · ·		
Río Cotopino	3	156-161 (158)		
Baños-Canelos			1	163
Sarayacu	1	161	1	167
Chiguaza	2	157-163 (160)		
Gualaquiza			1	157
Total	6	156–163 (159)	3	157–167 (162)

 TABLE V

 GEOGRAPHIC VARIATION IN VENTRAL COUNTS IN Atractus major From Ecuador

caudals, the female (BM 1933.6.24.99), 169 ventrals and 43 caudals. The color pattern is of type B according to J. C. Battersby. The scutellation of these snakes falls within the usual limits of the species, except that the male has a single postocular on the left side. This record is in some doubt since Loja is nearly 3000 feet (900 meters) higher than any other locality for the species. Also in the British Museum collections is a small male (BM 1933.6.24.100) from Zamora, Santiago-Zamora Province, with 156 ventrals and 40 caudals. The coloration is as in the Loja examples and lepidosis is typical of *Atractus major*.

A puzzling specimen (OV 728) is a small male, 231 mm. in standard length, from Santo Domingo de los Colorados, Pichincha Province. It has eight maxillary teeth, 155 ventrals, 42 caudals, six supralabials, and two postoculars. The color pattern is essentially similar to type D, except that posteriorly the bands tend to be broken up and fused into an irregular series of blotches. If the example from Intac discussed above is correctly labeled it may be that it belongs with the present specimen and they represent an undescribed western cognate of major. There seems to be no question concerning the locality data on the Santo Domingo snake. Aside from the marked differences in coloration between this specimen and the Intac example the two agree rather closely. They are different from all other major examined in having eight maxillary teeth (five, six, or seven in typical major). Under the circumstances it seems best to regard the status of the Santo Domingo specimens as doubtful. Reference to major presents a disconcerting geographic pattern with the same form occurring on both the east and west slopes of the Andes. However, the differences between this specimen and the typical *major* are so slight as not to justify its description at this time as a distinct form. Only future collecting in western Ecuador can satisfactorily settle the status of the Santo Domingo *Atractus*.

DISTRIBUTION.—Found throughout the forested Oriente region of Ecuador (Fig. 9) between 600 and 3500 feet altitude (200–1100 meters). Specimens very similar to *Atractus major* in scutellation and coloration occur along the upper margins of the Amazon basin in Venezuela, Colombia, Perú and Bolivia. Whether these areas all support populations identical with Ecuadorian ones cannot be determined at this time.

MATERIAL EXAMINED. – "Oriente": Turula (AM 32966-69); Napo-Pastaza: Abitagua (UM 89026, 92033, 94067); headwaters of Río Arajuno (OV 612); Baños to Canelos (AM 35893); Río Cotopino (UM 92032, 92036, 94068); Río Pastaza (UM 89005-06); San Francisco, 4mi. (6 km.) SEE of Puyo (JAP 2053); Sarayacu (AM 28790, UM 89024); Río Talín (OV 720-21); Villano (OV 722); Santiago Zamora: Chiguaza (OV 651-52); Gualaquiza (AM 35191); Macas (AM 35825, 35841, 35844-46, 35859-61, 37928); Riobamba-Macas Trail (AM 15201-05, 23257, 23260, 23263, 23265, 23267, 23271, 23287, 23292, 23299, 23311, 23314, 23319, 25931, 25933, 25936-38, 25946, 28818, 28820); Tunguarahua: Mapoto (UM 89025); San Francisco de Mapoto (UM 89023).

ADDITIONAL MATERIAL.—Forty specimens of *A. major* not seen by me are in the Escuela Politecnica Nacional, Quito. Several specimens in the British Museum examined for me by J. C. Battersby are included with the Quito material in the following list: *Loja*: 2 miles east of Loja (BM); *Napo-Pastaza*: Arajuno; Avila; Chicherota; mouth of Río Coca; Concepcíon; Río Copataza; Río Corrientes on trail between Montalvo and Conambo; Río Guataracu; Loreto; between Loreto and Payamino; Sarayacu; lower Río Suno; Río Talín; Villano; *Santiago-Zamora*: Chiguaza; Macuma; Zamora (BM).

Atractus microrhynchus (Cope, 1868)

Rhabdosoma microrhynchum Cope (1868: 102; type locality, Guayaquil, Guayas Province, Ecuador).

The original description of this form is totally inadequate to distinguish it from any other unicolor *Atractus* with a light collar. The holotype (AP 6693) is not at Philadelphia or Washington and is presumed to be lost. The type locality (Fig. 7) is in a region (the north coastal plain) from which no members of the genus except the banded *Atractus multicinctus* have been taken. If the locality is accepted, and there seems to be no reason why it should not be, it is probable that *microrhynchus* is a valid form not retaken since its original discovery by the Orton Expedition. In the less likely event that the locality data are in error in detail, but the snake is Ecuadorian, there is the possibility that Cope had a representative of either Atractus paucidens or A. occidentalis. If the specimen was not taken in Ecuador there is very little hope of ever being able to apply Cope's name to a particular population within the genus. In any event, no attempt can be made to allocate the name at this time and it may be considered a nomen dubium. Additional collecting for Atractus along the northern coastal portion of Ecuador could resolve this problem.

Cope's original description is quoted below for comparison with the other forms discussed in this report. "Seventeen series of scales; supralabials seven, the first very small, the third and fourth entering the orbit. Prenasal larger, very nearly reaching lip. Prefrontals very small, equal postnasal, one-sixth the size of postfrontals. Latter longer than broad. Rostral contracted above by approach of prenasals. Loreal very long. No preocular, on one side two, on the other one postocular. Last upper labial longer than high. First pair of labials united; two pair only in contact with genials. Frontal subtriangular; occipitals elongate. Temporals 1–2. Total length 4 in. 7.5 lin.; tail 8 lin.

"Coloration like that of a *Tantilla*. Above dark brown, beneath pale brown, with a faint line along margins of the gastrosteges. Top of head blackish, brown behind; a partially complete yellow collar, which widens at the angle of the jaws. A deep brown band from eye to angle of mouth; upper labials yellow brown edged.

"Tail slender acute.

No. 6693, from Guayaquil. Nearest the R. badium D.B."

Atractus modestus Boulenger

Rhabdosoma crassicaudatum Günther (1859: 411; list; specimen later made type of new Ecuadorian species).

Atractus modestus Boulenger (1894: 304; type locality, west Ecuador); do Amaral (1929: 188; range).

DIAGNOSIS.—A puzzling *Atractus* having the loreal much shorter than in any other Ecuadorian member of the genus, except *Atractus elaps*. Readily determined by having the following combination of characteristics: (1) 17 scale rows; (2) a short loreal; (3) nine maxillary teeth; (4) ventrals in male holotype 173, probably about 10 higher in females; and (5) uniform dorsal coloration.

LEPIDOSIS.—Rostral small. Internasals small. Prefrontals long. Two postoculars. Temporals 1 + 2. Supralabials six, third and fourth enter orbit. Four infralabials meet each chin shield. Caudals in only known specimen, a male, 38; ventrals plus caudals, 211. HEMIPENES.-J. C. Battersby reports that the hemipenes are differentiated and not unlike those of *Atractus major*. The base is covered with the usual short plicae. The central spinous region is abruptly demarcated from distal region which is covered with small papillate structures. The sulcus spermaticus divides at the level of the eighth caudal and the organ extends to caudal number 10.

COLORATION.—Uniform grayish above; ventrally yellowish on mid-line, but lateral portions of ventrals suffused with gray as is underside of tail.

MEASUREMENTS.—The holotype of the species is 330 in standard length; tail length, 50. Tail length as a percentage of standard length, 15.

REMARKS.—The status of this distinctive form is problematical. The holotype is unique among all *Atractus* having a small rostral, small internasals, and long prefrontals, in the possession of a rather short loreal shield. In the latter character *modestus* approaches the red and black ringed species, *Atractus elaps* and *Atractus latifrons*, from which it is distinguished in the essential features of the head scales (the ringed species have a large rostral, large internasals, and broad prefrontals), hemipenes (undifferentiated in *elaps* and *latifrons*), and coloration. In rare instances examples of *Atractus* with typically long loreals may have one or both of the loreals reduced in size. It is probable that the type of *modestus* is an aberrant specimen of this kind from a population characterized by a long loreal.

The type locality of "west Ecuador" is subject to the usual question of reliability connected with British Museum material collected by Fraser. Without evidence to the contrary it is assumed that the species is from western Ecuador.

DISTRIBUTION.-Known only from western Ecuador.

Atractus multicinctus (Jan)

Rhabdosoma multicinctum Jan, (in Jan and Sordelli, 1865, Pl. 4, Fig. 5; type locality, Lima, Departamento de Lima, Perú; in error).

Atractus multicinctus Boulenger (1898: 116; recognized as distinct from Atractus badius; specimens from Paramba, Imbabura Province, Ecuador); Boulenger (1913: 1035; specimen from Peña Lista, Condoto, Departamento de Chocó, Colombia).

DIAGNOSIS.—Superficially similar to Atractus major of eastern Ecuador, but distinguished from that species and other members of the genus in Ecuador as follows: (1) 17 scale rows; (2) long loreal; (3) maxillary teeth five or six; (4) ventrals in males, 168–183 (175), in females, 177–184 (179); and (5) banded pattern.

LEPIDOSIS.—Rostral small. Internasals small. Prefrontals long. Two postoculars. Temporals 1 + 2. Supralabials seven, third and fourth enter orbit. Infralabials six, three meet each chin shield. Caudals in males, 40-43 (41), in females, 31-36 (33); ventrals plus caudals, 208-226 (214).

HEMIPENES.—Organ similar to that of *A. major*; basal portion with plicae upon which are located several small spines. An elongate naked pocket extends from the plicate area toward tip, reaching about halfway to level of sulcus division. At about level of second caudal, plicae merge with a series of hooked central spines. Spines cover most of central portion of organ distal to plicae; abruptly replaced just before sulcus division by small papillate flounces that cover the remainder of hemipenis. Sulcus spermaticus divided at level of fourth caudal. Organ differentiated, reaching to eighth or ninth caudal.

COLORATION.—Dorsal ground color light, with a series of 15 to 21 wide brown blotches superimposed upon it. Blotches cover ground color to a degree that creates impression of alternating light and dark transverse bands. Light interspaces, 31–43, irregular, about two scale rows in longitudinal extent. Parietal region, lips, and throat light, rest of head dark brown. Belly light, immaculate except where dorsal dark bands infringe on upper edges of ventrals. Underside of tail heavily mottled with black.

MEASUREMENTS.—In my sample of three males and three females the standard length is 262-354 (299). Males: standard length, 262-300 (284); tail length, 42-51 (45); head length, 6-8 (7); head width, 6. Females: standard length, 286-354 (314); tail length, 32-42 (36); head length, 7-9 (8); head width, 5-6 (5.2). In percentages of standard length these measurements have the following ranges: Males: tail length, 15-16; head length, 2-3; head width, 2-2.3. Females: tail length, 10-12; head length, 2.3-2.8; head width, 1.4-2.1.

REMARKS.—The application of the name *multicinctus* to an Ecuadorian form is subject to some doubt. The species was originally described from Lima, Departamento de Lima, Perú, apparently in error (Jan and Sordelli, 1865). Boulenger (1898 and 1913) revived the name for material from northwestern Ecuador and the Colombian Chocó. An examination of the original plate of the species confirms the great similarity between the type specimen and the Ecuador-Colombia population. It thus seems very likely that Boulenger's allocation is correct. Rediscovery of *multicinctus* in Perú would, however, necessitate a reconsideration of the status of the material referred to that name in this paper.

Although the species is amply distinguished from Atractus major by ventral and caudal counts, dentition, size, and coloration, and although the two forms do not appear to be directly related, occasional examples of major from the Pastaza Cañon region of Amazonian Ecuador approach

multicinctus in certain characteristics. The primary difficulty here stems from a number of specimens of major having the usual blotched pattern of the species, modified into a series of dark transverse bands which alternate with the light interspaces representing the ground color (described as pattern D in the account of major). In this respect these snakes resemble rather closely typical multicinctus. There is also some overlap in other features between Pastaza major and the west coast form. However, Atractus multicinctus consistently has a higher ventral count, 168-183 (175) in males, 177-184 (179) in females; a higher ventral plus caudal count, 208-226 (214), fewer teeth on the maxillary (five or six), a smaller adult size, maximum in males, 300 mm., in females, 354 mm., and a color pattern of transverse cross-bands. Specimens of major from the Pastaza Cañon area may resemble *multicinctus* in one or two of these characteristics, but are always different in the others. Comparable data for comparison with multicinctus are given below for the Pastaza series of major. Ventral count in males, 163-172 (166.5), in females 171-181 (177); ventrals plus caudals, 196-221 (210); maxillary teeth usually seven; maximum standard length of males, 417 mm., of females, 565 mm.; and the color pattern is usually of irregular dark blotches. No difficulty is encountered in separating multicinctus from Atractus major from the vicinity of Macas or the lowlands of eastern Ecuador. These latter examples always have fewer ventrals than multicinctus, 148-163 (157) in males and 157-173 (164) in females; fewer ventrals plus caudals, 188-217 (197); usually six teeth on maxillary, sometimes five; a larger adult size, maximum standard length in males, 512 mm., in females, 852 mm.; and the coloration is always of blotches.

It is doubtful that the approach of certain examples of the eastern lowland form, *Atractus major*, to individuals of the western lowland species, *Atractus multicinctus*, are indicative of any direct genetic connection between the two populations. Although the two species are members of the *Badius* Group, any close relationship between them would probably have to be established on the basis of a series of intermediate Colombian populations. The Andes of Ecuador appear to prevent any contact at present between these two relatively low altitude forms.

Possible allies of *A. multicinctus* in western Ecuador may be represented by two *major*-like specimens labeled Intac, Imbabura Province, and Santo Domingo de los Colorados, Pichincha Province. Neither of these snakes resembles *multicinctus* to any great degree and both appear to be much closer to *Atractus major*. The specimens in question are described and discussed in detail under the latter name.

DISTRIBUTION.-Found in the dense tropical forests of the northwest coastal region of Ecuador (Fig. 9) and northward into the Colombian

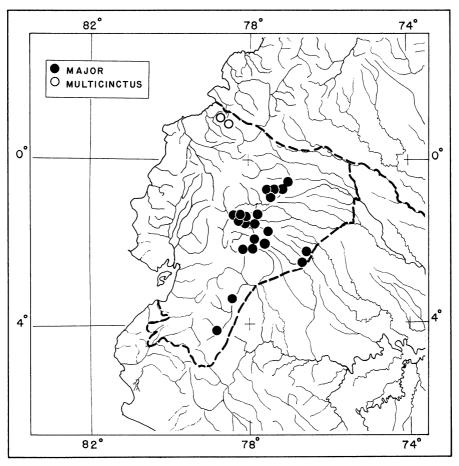


FIG. 9. Geographic distribution of Ecuadorian members of the *Badius* Group of *Atractus*.

Chocó. Specimens have been collected at elevations between 100 and 2500 feet (50-800 meters).

MATERIAL EXAMINED.—*Esmeraldas*: San Javier (BM 1903.3.29.31). *Imbabura*: Paramba (CM 11587–88; MC 8083, 13275; UM 51259).

Atractus occidentalis Savage

Atractus badius Fowler (1913: 168; two examples from Huigra, Chimborazo Province, Ecuador).

Atractus occidentalis Savage (1955; type locality, Mindo, Pichincha Province, Ecuador).

DIAGNOSIS.-A form showing closest similarity in coloration to Atractus

ecuadorensis and in scutellation to A. dunni, but differing from them and other Ecuadorian Atractus in: (1) 17 scale rows; (2) long loreal; (3) maxillary teeth six or seven; (4) ventrals in male, 153, in females, 162; and (5) pattern of irregular or disrupted longitudinal stripes.

LEPIDOSIS.—Rostral small. Internasals small. Prefrontals long. Postoculars two (84 per cent) or three (16 per cent). Temporals 1 + 2. Supralabials seven, third and fourth enter orbit. Infralabials six, three or four meet each chin shield. Caudals in male, 39, in females, 26–27 (26.5); ventrals plus caudals, 188–192 (189).

HEMIPENES.—Organ covered with larger spines near center and with small spines toward base and tip. Basal plicae with small hooked spines. Lateral pocket reaches level of fourth caudal. Pocket opposite sulcus spermaticus; sulcus divides at seventh caudal. Hemipenes reach to 18th caudal.

COLORATION.—The color pattern of the male holotype (BM 1916.5.23.5) is as follows: dorsal ground color brown with six irregular longitudinal stripes of darker brown. A pair of dorsolateral stripes, corresponding to dorsolateral blotches of Atractus gaigeae, on sixth and seventh scale rows; a pair of lateral stripes on portions of third and fourth or fourth and fifth scale rows; and a pair of lateroventral stripes on parts of first and second scale rows. No definite ventral stripes although tips of ventral scutes marked with dark pigment. Light collar on neck not sharply demarcated posteriorly by a dark area, suffused with brown, the two lateral arms narrowly separated on the mid-dorsal line by a dark brown area and involving posteriolateral portions of parietals. Top of head dark brown, sides lighter, except for dark line through eye along upper edges of supralabials. Lower halves of supralabials light; throat and chin light with brown spots on anterior infralabials, chin shields, and mental. Belly light anteriorly, clouded with dark brown markings which are most concentrated laterally. At level of 110th ventral clouding comes to overlie most of the venter. Anal plate brown. Underside of tail dark brown with a few light punctations.

Two additional specimens (AP 18114 and 26316) from near Huigra, Chimborazo Province, are referred to A. occidentalis primarily on the basis of scutellation. They differ somewhat in coloration from the holotype as follows. Dorsal pattern of short longitudinal bars or stripes of dark brown on a light brown ground color. These spots tend to be regularly arranged and apparently are homologous to the irregular longitudinal lines on the holotype of the species. Spots in the following symmetrical series: a series of bars on sixth and seventh scale rows, corresponding to the dorsolateral stripes; a series on the fourth and fifth scale rows, corresponding to the lateral stripes. No indication of vertebral, lateroventral, or ventral stripes. Dark bars very narrow, much less than a scale row wide, usually two or three scales in longitudinal extent. Some scales associated with dark bars light, giving impression of a number of very small light spots scattered over dorsal surface. Top of head light brown, speckled with much light pigment, sides relatively light with a definite dark brown postocular stripe on lower parts of temporals and upper tips of posterior supralabials. Lower portions of supralabials light; chin and throat almost immaculate except for large brown spots on chin shields, infralabials, and mental. Belly overlain with a rich dark brown, numerous light spots and mottlings, particularly along mid-line. Anal plate same color as belly. Underside of tail brown with many small light punctations.

MEASUREMENTS.—The three available specimens are 112, 265, and 315 in standard length. The male holotype has the following measurements: standard length, 265; tail length, 56; head length, 9; head width, 5. The adult female has: standard length, 315; tail length, 35; head length, 10; head width, 5. These measurements expressed as percentages of standard length are: Male: tail length, 21; head length, 3.4; head width, 1.9. Female: tail length, 11; head length, 3.2; head width, 1.6. The very young female has not been included in calculating these proportions.

REMARKS.—Atractus occidentalis appears to be the western Ecuadorian representative of A. ecuadorensis, which it resembles in coloration. The new form is easily distinguished from ecuadorensis by the number of teeth, ventrals, and the length of the hemipenes. Very likely the relationship between these forms is not a direct one, but lies through populations of non-Ecuadorian forms to the north.

The specimens from the vicinity of Huigra, Chimborazo Province, are referred to *occidentalis* with some reservation. Although they agree closely with the type of the species from Pichincha Province in scutellation, the differences between the two samples in coloration are quite striking. However, I am reluctant to propose a new name on the basis of the slight difference in pattern, particularly in the light of the obvious close affinity between the two populations and the fact that the pattern of the southern individuals appears to represent the further development of trends indicated in the northern example. Perhaps when additional material is obtained segregation of the two populations might be justified at the subspecific level.

DISTRIBUTION.—Found along the lower slopes of the western Andes of Ecuador (Fig. 7) from the latitude of Quito to the latitude of the Hoyo dc Chimbo, at elevations of 2500 to 4100 feet (800-1200 meters).

JAY M. SAVAGE

MATERIAL EXAMINED. – Chimborazo: Huigra (AP 18114); between Huigra and Río Chiguancay (AP 26316). Pichincha: Mindo (BM 1916.5. 23.5), holotype.

Atractus occipitoalbus (Jan)

Rhabdosoma occipitoalbum Jan (1862: 16; type locality, western Ecuador); Jan and Sordelli (1865a, Pl. 2, Fig. 4).

- Atractus duboisi Boulenger (1880: 44; type locality, Andes of Ecuador); Boulenger (1894: 310; description; specimen from Intac, Imbabura Province, Ecuador); do Amaral (1929: 186; range); Savage (1955: 18; specimen from Sucúa, Santiago-Zamora Province, Ecuador).
- Atractus occipitoalbus Boulenger (1894: 310; description, listed from west Ecuador); Peracca (1897a: 17; list); do Amaral (1929: 188; range); Savage (1955:18; comparisons).

Atractus orcesi Savage (1955: 17; type locality, Loreto, Napo-Pastaza Province, Ecuador).

DIAGNOSIS.—A distinctive member of the *Trilineatus* Group, differing from all other Ecuadorian forms in: (1) 15 scale rows; (2) long loreal; (3) maxillary teeth seven or eight; (4) ventrals in males, 137–153 (147), in females, 150–171 (158); and (5) dorsal coloration uniform dark brown or black, or with several dark longitudinal stripes on a lighter ground color.

LEPIDOSIS.—Rostral small. Internasals small. Prefrontals long. One (36 per cent) or two (64 per cent) postoculars. Temporals 1 + 2. Supralabials seven (46 per cent) or eight (54 per cent), fourth and fifth or rarely third and fourth enter orbit. Infralabials six (90 per cent) or seven (10 per cent), four or rarely three or five meet each chin shield. In one example of this form the mental meets the chin shields. Caudals in males, 21-32 (25), in females, 9-19 (13); ventrals plus caudals, 158-187 (172).

HEMIPENES.—Organ covered with spines of nearly uniform length except at extreme base. Basal plicae small, surmounted by small spines that gradually grade into those on body of organ. Lateral pocket reaches to level of fifth or sixth caudal. Sulcus spermaticus divides at seventh caudal. Organ extends to level of caudal number 12.

COLORATION.—The majority of the examples examined are uniformly dark brown or black above. Usually a broad white collar on neck, which involves most of parietals and several nuchal scale rows. Collar suffused with dorsal color in some examples. Top and sides of head dark, with upper lip margins light. Belly usually dark, but may be light with a single midventral dark stripe. Throat and chin light with a few dark spots. Underside of tail dark.

Occasional specimens of this form retain a striped pattern. This condition is most pronounced in the example (SU 15622) from Loreto, Napo-Pastaza Province, described (Savage, 1955) as a distinct form, *Atractus* orcesi. In this snake the ground color is brown, with a series of dark longitudinal stripes; a single irregular vertebral stripe; a pair of lateral stripes on upper half of second and lower portion of third scale rows; and a pair of ventral stripes on tips of ventrals and lower edges of first scale row. The remainder of the pattern is essentially the same as in typical occipitoalbus except that the head is lighter brown and shows some dark and light markings. This example also has a definite mid-ventral stripe.

Less conspicuously different from uniformly colored occipitoalbus specimens is the example (EP 611) from Sucúa, Santiago-Zamora Province, referred to Atractus duboisi (Savage, 1955). This snake is a rich brown with a few light spots scattered down the sides. A definite ventral dark stripe is present along the tips of the ventrals and the lower portion of the first scale row. In other characters of pattern it is similar to the Loreto specimen.

Boulenger's (1880:44) holotype of *Atractus duboisi* is apparently an example similar to the Sucúa snake, except that the ground color is black instead of brown.

Several specimens of *occipitoalbus* from different localities exhibit evidences of the dark ventral stripe on the ventrals and first scale rows. In all other details of the pattern they agree with the uniformly colored specimens described above. Thus, it would seem that there is a complete transition from a striped condition through examples with reduced striping to the uniform coloration of the majority of *occipitoalbus* individuals. There does not appear to be any difference in scale counts or measurements between typical uniform examples and specimens having the stripes well developed.

MEASUREMENTS.—The standard length of the material examined is 93–298 (223), and is comprised of seven males and 14 females. Males: standard length, 93–269 (189); tail length, 10–38.5 (20); head length, 5–8 (7); head width, 3–4.5 (4). Females: standard length, 135–298 (239); tail length, 8–21 (12); head length, 6–8.5 (6.5); head width, 3.5–6 (4.4). These measurements expressed as percentages of standard length exhibit the following ranges of variations: Males: tail length, 10–14; head length, 3–3.9; head width, 1.5–2.4. Females: tail length, 3.8–8; head length, 1.9–3.2; head width, 1.8–2.6. A young male, 93 mm. in standard length, was not used in calculating these proportions.

REMARKS.—The names Atractus duboisi Boulenger and A. orcesi Savage are here placed in the synonymy of A. occipitoalbus (Jan). The three nominal forms differ only in color pattern. As shown in the section on coloration, intermediate patterns indicate that the types of each name merely represent diverse stages in the variational range. At the time of the description of orcesi, I was under the impression that the form had a higher number of ventrals (153 in the male holotype) than are found in occipitoalbus. New material, however, shows that uniformly colored examples also have this high a count. The only difference between *duboisi* and *occipitoalbus* is in the presence of small regularly arranged light lateral spots in the former. The specimen (EP 611) from Sucúa, Santiago-Zamora Province, referred by me (Savage, 1955) to *duboisi* agrees with the type except that its ground color is light brown, about the same as in the type of *orcesi*. None of these color differences by themselves warrant specific recognition and it seems best to consider the diverse patterns as all forming part of the variation within a single population.

The specimen (BM 78.1.25.33) from Intac, Imbabura Province, placed by Boulenger (1894) in Atractus duboisi, differs somewhat from typical A. occipitoalbus. This snake, a small female, has 170 ventrals, 16 caudals, six maxillary teeth, and a pattern similar to that of the holotype of *duboisi*, with a black ground color and small light dorsal spots arranged in a pair of parallel series down the sides. The ventral count in this example is near the maximum for occipitoalbus females (150-171) and all eastern Ecuadorian specimens of the species seen by me have seven or eight maxillary teeth. In the light of these characters it is difficult to evaluate the status of this individual. The snake was obtained by Buckley and sold to the British Museum; the locality data are dubious (see gazetteer for a more detailed discussion). Most likely the specimen is mislabeled and was actually taken in eastern Ecuador. However, the possibility remains that there exists on the west slopes of the Andes, near Intac, an undescribed form resembling occipitoalbus. Until the locality is verified I prefer to reject this suggestion and place this rather peculiar example with occipitoalbus...

DISTRIBUTION.—The upper Amazonian forests of eastern Ecuador (Fig. 6) between 600 and 3500 feet (200–1100 meters).

MATERIAL EXAMINED.—Napo-Pastaza: Abitagua (UM 92035); Arajuno (OV 68-69); Loreto (OV 603-05, SU 15622, holotype of A. orcesi); headwaters of Río Bobonaza (OV 606); San Francisco, 4 mi. (6 km.) SSE of Puyo (JAP 2054); Villano (EP 423, OV 725). Santiago-Zamora: Chanala-Macas Trail (AM 35928), Chiguaza (OV 607); Macas (AM 28824), 35847-49, 35852-53, 35855, US 65481); Mendez (OV 66-67); Sucúa (OV 611).

Atractus paucidens Despax

Atractus (Atractopsis) paucidens Despax (1910: 372; type locality, Santo Domingo de los Colorados, Pichincha Province, Ecuador; type of new subgenus); Despax (1911: 31, Pl. 2; redescription, figures of entire snake, dorsal and lateral views of head and maxillary dentition).

DIAGNOSIS.—A uniformly colored member of the *Trilineatus* Group from western Ecuador, most obviously allied to *Atractus occidentalis* from which

it differs in coloration and in having more ventrals and caudals. Well distinguished from other Ecuadorian *Atractus* by: (1) 17 scale rows; (2) long loreal; (3) five (?) or six maxillary teeth; (4) ventrals probably about 168 in males, in two female specimens, 169–186 (178); and (5) dorsally, a uniform gray or dark brown.

LEPIDOSIS.—Rostral small. Internasals small. Prefrontals long. Two postoculars. Temporals 1 + 2. Supralabials six or seven, third and fourth enter orbit. Infralabials six, four meeting each chin shield. Caudals probably about 44 in males, in females, 31-37 (34); ventrals plus caudals, 200–223 (216.5).

HEMIPENES.-No males known.

COLORATION.—Dorsum gray or dark brown, except for lower half of first scale row which is light on anterior portion of body. Some dark punctations even on these light scales. Light nuchal collar indicated, but overlain with dark pigment and not crossing completely over the mid-line. Postnuchal dark area clearly sets off light collar, although dark area may be reduced or absent on mid-line. Head dark above. Lower margins of upper lips light, rest of side of head dark. Throat and chin light, with definite dark spots on mental, infralabials, and chin shields. Belly light with definite dark spots at posteriolateral corner of each ventral, at least on anterior portion of body. On posterior portion of body, spots expanded and lateral edges of ventrals heavily mottled with dark brown. In holotype of species, belly uniform gray. Anal and underside of tail dark brown or gray, with a few light flecks.

MEASUREMENTS.—Standard length and tail length of the holotype and a second specimen are 320 and 43, and 266 and 35, respectively. Measurements on the latter example: head length, 8; head width, 5. Both of these snakes are females. Proportions expressed as per cent of standard length: tail length, 13 (in both examples); head length, 3; head width, 1.9.

REMARKS.—This species was described by Despax (1910) on the basis of a single female now in the Paris Museum. Despax made *paucidens* the type of a distinct subgenus of *Atractus* primarily on the grounds that his specimen had only four maxillary teeth. Examination of his 1911 figure of the maxillary bone clearly shows that although only four teeth are present, the maxillary is incomplete and possibly broken. Only the anterior two-thirds of the jaw are illustrated and it seems likely that at least one and possibly two teeth would have been present on the missing third of the bone. There is no valid reason for separating this species from the other members of the genus, either on the basis of dentition or any other characters. Therefore, the subgenus *Atractopsis* Despax, 1910, is not recognized in this report.

A second female (OV 708) from the Esmeraldas drainage of western

Ecuador is here placed in *A. paucidens*. It differs slightly from the type in having fewer ventrals and caudals (169 + 31 versus 186 + 37 in the holo-type) and in details of coloration. The locality from which this snake was taken is about 40 miles north of the type locality for the species.

Although Atractus paucidens is placed in the Trilineatus Group of the genus in this report, final allocation must await examination of the hemipenes. The characteristic light collar and general coloration suggest trilineatus and its allies; however, paucidens is also very similar to Atractus multicinctus of the Badius Group in longitudinal counts, tail proportions, and maxillary dentition. A. multicinctus is a banded species from northwestern Ecuador and might eventually prove to be allied to paucidens. The possibility exists that the species may be nothing more than a northern uniformly colored representative of Atractus occidentalis. At the present time I favor the latter hypothesis.

DISTRIBUTION.—Atractus paucidens is known from two localities along the slopes of the Andes in northwestern Ecuador (Fig. 7). The type locality, Santo Domingo de los Colorados, Pichincha Province, is at an elevation of 1625 feet (500 meters). The second specimen is from near the mouth of the Río Pitzara, but from Pichincha Province, at an elevation of about 800 feet (250 meters). Both specimens are from the tropical forest belt.

SPECIMEN EXAMINED.—*Pichincha*: near mouth of Río Pitzara (OV 708). The Pitzara empties into the Río Guaillabamba within the boundaries of Esmeraldas Province.

Atractus resplendens Werner

Atractus torquatus var. resplendens Werner (1901: 598; type locality, Ecuador).

DIAGNOSIS.—A member of the *Trilineatus* Group readily distinguished from the other known *Atractus* by the following combination of characters: (1) 17 scale rows; (2) long loreal; (3) maxillary teeth seven; (4) ventrals in males, 157–174 (166), in females, 170–185 (176); and (5) dorsal body color a uniform dark brown or black.

LEPIDOSIS.-Rostral small. Internasals small. Prefrontals long. Postoculars one (86 per cent), two (10 per cent) or fused with fifth supralabial (4 per cent). Temporals 1 + 2. Supralabials seven (21 per cent), eight (77 per cent), or nine (2 per cent), third and fourth, fourth and fifth, or fifth and sixth enter orbit. Infralabials five (3 per cent), six (95 per cent), or seven (2 per cent), usually four, rarely three or five, in contact with each chin shield. Caudals in males, 25–31 (29), in females, 14–19 (16); ventrals plus caudals, 182–203 (193).

HEMIPENES.-Whole organ covered with spines of about equal length except at extreme base; smallest spines toward base, largest near middle.

Basal plicae rather large, each with a row of small spines. Lateral pocket reaches level of sixth caudal. Sulcus spermaticus divides at level of eighth caudal. Each hemipenis extends to level of 13th caudal.

COLORATION.—Back uniformly brown in aspect, but each scale with a few light punctations medially. A faint vertebral stripe usually indicated. Light collar on neck usually obscured by dark brown, although frequently strongly evident; often restricted to lateral portion of neck and a remnant represented by light spots on tips of parietals. Head dark brown or gray, with lower edges of supralabials lighter. Throat light, but mental, infralabials, and chin shields heavily spotted with dark brown, and gular scales edged with brown. Belly light, but usually flecked with dark spots; sometimes dark spots fused and expanded so as to obliterate almost completely light color; latter usually retained on edges of ventrals and as an irregular mottling on centers of ventral scutes. Underside of tail entirely dark or with a few light areas.

MEASUREMENTS.—The material available comprises 10 males and 18 females with a standard length of 119–372 (236). Males: standard length, 119–337 (186); tail length, 12–42 (21); head length, 5–9 (6.6); head width, 4–6 (4.6). Females: standard length, 137–372 (269); tail length, 9–27; head length, 6–9.5 (7.9); head width, 4.5–6.5 (5.2). Proportions as percentages of standard length are: Males: tail length, 10–12; head length, 2.6–4.5; head width, 1.8–3.5. Females: tail length, 5.5–8.2; head length, 2.4–4.7; head width, 1.6–3.4. Three males under 130 mm. in standard length were not used in calculating the proportions.

REMARKS.—In the past this distinctive form has been confused with several populations to which the name *Atractus torquatus* (Duméril, Bibron, and Duméril, 1854) has been applied. In part, this confusion stems from the history of the name *torquatus*.

The binomen *Brachyorrhos torquatus* was first published by F. Boie (1827: 540) on the basis of information contained in the great unpublished work, *l'Erpetologie de Java*, prepared by H. Boie. Although the species is listed as being from the Indian Archipelago, no indication of its characteristics are given. Therefore, the name presented in this context must stand as a *nomen nudum*.

Wagler (1830: 35) listed this species under *Brachyorrhos*, but provided no information regarding its characteristics.

Schlegel (1837: 35) regarded Boie's torquatus as a synonym of Calamaria babia Schlegel from French Guiana, but gave no suggestions as to the distinctive features of the former. Schlegel's usage did not constitute valid publication according to the International Rules of Zoological Nomenclature (see Hemming, 1953: 63). Duméril, Bibron, and Duméril (1854: 101) utilized this name in the combination *Rhabdosoma torquatum* for material of *Atractus* from French Guiana and Bolivia. Their work must stand as the original place of publication of the specific name under the International Rules. Unfortunately, it is obvious that their description is composite, the single Bolivian specimen being well distinguished from Guianan material. Therefore, in order to avoid any future confusion regarding the allocation of the name torquatus, I herewith designate as the lectotype of *Rhabdosoma torquatum* Duméril, Bibron, and Duméril, the Bolivian syntype utilized in the preparation of their description.

The lectotype of *torquatum* is in the Paris Museum, number 437. It is a male with 17 scale rows, 148 ventrals, an incomplete tail, and eight supralabials, with the fourth and fifth supralabials entering the orbit. The pattern consists of a series of dark transverse bands on a lighter ground color. There are two pairs of dark blotches, one set on the posterior region of the head and the other on the neck, emphasizing the light nuchal interspace to give the impression of a light collar. The type locality of the species is Santa Cruz, Santa Cruz, Bolivia.

Boulenger (1894: 309) referred two specimens from Demerara Falls, British Guiana, to *Atractus torquatus*. They appear to be in essential agreement with the French Guianan material of Duméril, Bibron, and Duméril. Boulenger's material is not conspecific with the Bolivian form, but the exact status of the Guiana specimens cannot be determined at this time.

Atractus resplendens differs from both populations previously referred to A. torquatus in its uniform coloration. From the Bolivian form it is further distinguished by having more ventrals (170–185 in male resplendens, 148 in the lectotype of torquatus). The caudal counts are much lower in A. resplendens than in Guianan material previously placed in torquatus (25–31 in males, 14–19 in females of the Ecuadorian form versus 43 in the male and 41–43 in females from the Guianas). It appears likely that further investigations will place the Guianan and Bolivian forms in the Badius Group of species, distinguished by having differentiated hemipenes, while A. resplendens definitely falls into the Trilineatus Group in which the hemipenes are undifferentiated.

The holotype of *resplendens* has 165 ventrals and 15 caudals. If, as the number of caudals suggests, this example is a female, then the ventral count is well below any in my series. On the other hand the type may be a male with a portion of the tail missing. Unfortunately, no specific locality data are available for this example and the possibility remains that the type may have come from a population differing slightly from the material employed

in this study. Until additional examples are taken it appears best to place all specimens under the single name.

DISTRIBUTION.—Found along the eastern slopes of the Andes of Ecuador (Fig. 7) at elevations between 3500 and 6200 feet (1100–1900 meters).

MATERIAL EXAMINED.—Ecuador: (MC 29295). Chimborazo: eastern portion (AM 35974–79). Santiago-Zamora: Normandia (AM 28787); Riobamba-Normandia Trail (AM 35932). Tungurahua: Baños (SU 8246, UM 89010–19); Río Pastaza (UM 84108, 89007–09); Rutun Hill (CM 28018–20, 28030–31), Yunguilla (CM 28021).

Atractus roulei Despax

Atractus roulei Despax (1910: 370; type locality, Alausí, Chimborazo Province, Ecuador); Despax (1911: 30, Pl. 2; redescription, figures of entire snake, dorsal and lateral views of head).

DIAGNOSIS.—A well-demarcated species of Atractus most obviously similar to A. carrioni of southeastern Ecuador. Readily distinguished from other Atractus by: (1) 15 scale rows; (2) long loreal; (3) maxillary teeth, 10-11; (4) ventrals in males, 140-145 (143), in females, 145-149 (148); and (5) uniform dark brown dorsally.

LEPIDOSIS.—Rostral small. Internasals small. Prefrontals long. One postocular. Temporals 1 + 2. Supralabials six, third and fourth enter orbit. Infralabials five, three meeting a chin shield on each side. Caudals in males, 20–26 (23), in females, 14–23 (18); ventrals plus caudals, 160–174 (167).

HEMIPENES.—Central portion covered with spines gradually increasing in size from plicate region to sulcus. Tip of organ with spines slightly smaller than central ones. Typical naked pocket and spinate basal plicae extend to level of third caudal. Sulcus spermaticus divides at level of fifth caudal. Organs undifferentiated, reach to level of tenth caudal.

COLORATION.—Uniform dark brown above and below, with a few obscure light blotches distributed randomly on belly. Lips light brown.

MEASUREMENTS.—The standard length of the sample of two males and four females is 116–396 (230). Males: standard length, 116–330 (223); tail length, 12–38.5 (35); head length, 7–11 (9); head width, 4–8 (6). Females: standard length, 125–396 (207); tail length, 12–31 (22); head length, 8–12 (10); head width, 4–6.5 (5). Measurements expressed as percentages of standard length are: Males: tail length, 10–12; head length, 3.3–6; head width, 2.4–3.5. Females: tail length, 7.4–7.8; head length, 3–4.9; head width, 1.5–2.5.

REMARKS.—Atractus roulei appears to be closely allied to A. carrioni of the Loja Valley in southeastern Ecuador. These two forms are similar in

general body proportions, scutellation, coloration, and dentition, but differ in the condition of the loreal shield (present in *roulei*, absent in *carrioni*).

Within the genus only two other nominal forms approach roulei and carrioni in having 15 scale rows and six supralabials. These snakes, Atractus boettgeri Boulenger (type locality, Las Yungas, Cochabamba, Bolivia), and Atractus taeniatus Griffin (type locality, Santa Cruz, Santa Cruz, Bolivia), are of uncertain status. Both names are based upon single specimens and may represent aberrant examples from populations typically having seven supralabials. Another factor affecting the possible relationships between these two species and the Ecuadorian forms lies in the nature of the number of scale rows around the body. It seems likely that forms with 15 scale rows have evolved from types with 17 scale rows and that the reduction from 17 to 15 has occurred several times and in several different species groups within the genus Atractus. A. boettgeri is rather similar to Atractus emmeli Boettger (type locality, Río Mapiri, La Paz, Bolivia) in all features except that the latter form has seven supralabials. A. taeniatus exhibits no close approach to any other described species with 15 scale rows. Until the hemipenes and dentition of these doubtful species have been examined it seems logical to include them in the same group with roulei and carrioni. The following key will serve to separate the four forms discussed above.

1a. A lorcal present, separating prefrontals from supralabials; no preocular. 2a. Two postoculars: four infralabials meeting each chin shield.

2a. I wo postoculars; four intralabilits meeting each chin shield.
3a. Ventrals plus caudals 197A. boettgeri
3b. Ventrals plus caudals 176A. taeniatus
2b. One postocular; three infralabials meeting each chin shield; ventrals plus
caudals, 160–174
1b. No loreal, prefrontals meeting supralabials; sometimes a small preocular; one
postocular; three or four infralabials meeting each chin shield; ventrals plus caudals,
174–179 A. carrioni

DISTRIBUTION.-Known only from the slopes of the Andes in southwestern Ecuador (Fig. 6) at altitudes between 4000 and 8600 feet (1200-2600 meters). The species may be expected from northwestern Perú.

MATERIAL EXAMINED.—Bolivar: San José del Chimbo (AM 17492) Chimborazo: Alausí Valley (US 33861–62). El Oro: El Chiral (AM 18325), Chonta (AM 22110–11).

REVISION OF Atractus

KEY TO THE ECUADORIAN SNAKES OF THE GENUS ATRACTUS

1 <i>a</i> .	Color pattern of red and black rings, sometimes with white or yellow rings as
	well; rostral large; internasals large; prefrontals broad
1b.	
	or uniformly colored, never of black and yellow rings; rostral small; internasals
	small; prefrontals long
2a.	Dorsal scales in 15 rows
2b.	Dorsal scales in 17 rows
3a.	No loreal, although sometimes with a minute preocular; prefrontals in contact
0.1	with supralabials
3b.	Loreal present, no preocular; prefrontals widely separated from supralabials 4
4a.	Light nuchal collar present, although sometimes suffused with dark pigment
	dorsally; seven or eight maxillary teeth
4b.	No light nuchal collar; 10 or 11 maxillary teeth
5a.	Ventrals plus caudals fewer than 175 (range 164–173)
5b.	Ventrals plus caudals more than 180 (range 182-240)
6a.	Uniform dark brown dorsally
6b.	Dorsal pattern of longitudinal dark stripes and a paired series of dark
_	blotches
7a.	Dorsal pattern of large irregular dark blotches or regular cross-bands
7b.	Dorsal pattern of stripes, small spots or dorsum uniform in color
8a.	Ventrals, 168 or more in males (range 168–183), 177 or more in females (range
	177-184); ventrals plus caudals, 208 or more (range 208-226); maxillary teeth
01	five or six; color pattern of transverse bands
8b.	Ventrals usually less than 168 in males (range 148–172), usually less than 177 in females (range 157–181); ventrals plus caudals usually less than 208 (range
	188–221); maxillary teeth usually six or seven, rarely five (in available examples approaching <i>multicinctus</i> in ventral counts the maxillary teeth are seven); color
	pattern usually of large irregular blotches, some examples with transverse
	cross-bands
9a.	Dorsum uniformly colored
9b.	Dorsum with a pattern of longitudinal dark stripes or small spots
10a.	Caudals in males fewer than 35 (range 25–31), in females fewer than 20 (range
1000	14–19)
10b.	Caudals in males more than 35 (38), in females more than 20 (range 31–37) 11
11a.	Maxillary teeth five or six; a light nuchal collar
11b.	Maxillary teeth nine; no light nuchal collar
12a.	Ventrals plus caudals more than 210 (range 222–240)
12 <i>b</i> .	Ventrals plus caudals less than 210 (range 185–196)
13a.	Ventrals in males, 150 or more (range 153–163), in females, 160 or more (range
	162–175); maxillary teeth five to seven
13b.	Ventrals in males less than 150 (144), in females, less than 160; maxillary teeth
	eight
14a.	Ventrals plus caudals, 194–196; maxillary teeth five; ventral stripes present
	A. collaris
14b.	Ventrals plus caudals, 188-192; six or seven maxillary teeth; no ventral stripes
	A. occidentalis

JAY M. SAVAGE

RELATIONSHIPS

The Ecuadorian members of the genus *Atractus* fall into three welldefined groups on the basis of hemipenial structure, dentition, scutellation, and coloration. The species included within each group resemble one another so closely that there can be no serious question regarding the naturalness of these subdivisions. A preliminary survey of a considerable number of non-Ecuadorian species indicates that known members of the genus belong to one or another of the groups characterized here. Further investigation may reveal additional species groups within *Atractus*, although no material examined in the preparation of this report suggests that there are more than three major groups.

The three principal groups of *Atractus* and their distinguishing characteristics are given in Table VI.

Character	Badius Group	Trilineatus Group	Elaps Group
Hemipenes Dentition	differentiated teeth conic; widely separated	undifferentiated teeth conic; widely separated	undifferentiated teeth strongly com- pressed; set close together
Rostral	small	small	large
Internasals	small	small	large
Prefrontals	long	long	broad
Loreal	long	long	short
Pattern	blotches, bands, or dorsum uniform	stripes, small dark or light dots, or dorsum uniform	alternating rings of red and black; sometimes white or yellow rings as well

TABLE VI

DISTINGUISHING CHARACTERISTICS OF PRINCIPAL GROUPS OF Atractus in Ecuador

It is not possible to evaluate fully the relationships between the three species groups at the present time. However, certain tentative conclusions may be expressed subject to modification as our knowledge of the extralimital species becomes more nearly complete.

The *Badius* Group differs markedly from the others in possessing differentiated hemipenes. In all other features except this, and coloration, the section agrees closely with the *Trilineatus* Group. The *Elaps* Group on the other hand is distinct from both the others in scutellation, dentition, and coloration, but it agrees with the *Trilineatus* Group in having undifferentiated hemipenes. On the basis of these data it must be concluded that the

Badius Group is most closely allied to the Trilineatus Group and can only be distantly related to *elaps* and its allies. While the *trilineatus* line appears to occupy a position intermediate between the other two groups, agreeing with badius and its relatives in scutellation and dentition and with the elaps stock in hemipenial characters, it is difficult to determine to which group it is most closely related. If it is borne in mind that the outstanding peculiarities of the Elaps Group in scutellation, dentition, and coloration are probably all modifications from any presumed Atractus ancestor, then the Trilineatus Group might best be placed near badius and its allies on the basis of their common primitive characteristics. If the hemipenial differences are emphasized, trilineatus and related species would have to be placed near *elaps*. At the present time the former view appears to be most satisfactory on the basis of the assumption that the hemipenial characteristics are not as profoundly significant as the combination of scutellational and dentitional features. Under this concept the Badius and Trilineatus groups are placed near one another with the *Elaps* Group being regarded as rather distantly related to them. The Trilineatus Group is considered to be more closely allied to the *elaps* stock than the latter group is to *badius* and its allies.

Without additional information on exotic species it is not worthwhile to attempt construction of any phylogenetic scheme purporting to illustrate the direction of evolution in Ecuadorian members of the genus. If the Elaps Group is accepted as being the most advanced stock then it follows that the badius line is the most primitive in that it differs most markedly from elaps and its allies. The Trilineatus Group must then be presumed to have been derived from a *badius*-like ancestor and *elaps* and related species from a trilineatus-like form. Less likely possibilities are: (1) undifferentiated hemipenes arose twice from differentiated ones and the Elaps and Trilineatus groups are not closely allied, but remain as independent parallel derivatives from the Badius Group; (2) the Trilineatus Group is' the primitive stock with the Badius Group arising from it through evolution of differentiated hemipenes and the Elaps Group through modifications in scutellation, dentition, and coloration. Further study may reveal which of these postulates is the more plausible, but it seems best to recognize the differentiated hemipenes as primitive and accept the hypothesis that the Badius Group is ancestral to the Trilineatus Group, which in turn apparently gave rise to the *elaps* line.

The degree of relationship between the various Ecuadorian species within each of the three groups cannot be estimated with any great accuracy at the present time. It is obvious that most species of Ecuadorian *Atractus* from the Amazonian side of the Andes will eventually prove to be more closely allied to other Amazonian species than to Pacific coastal forms. By the same token Ecuadorian forms of *Atractus* from the Pacific slope are most likely to have their nearest relatives occurring in coastal Colombia rather than in eastern Eucador. Determination of possible evolutionary patterns in each group cannot be undertaken, except perhaps in a general way, until our understanding of the genus outside the political boundaries of Ecuador becomes more nearly complete. Hence, discussion of relationships between species within the groups is restricted to a consideration of possible affinities to other Ecuadorian forms. No attempt is made to evaluate the possible course of phylogeny in this artificially delimited segment of the genus *Atractus*.

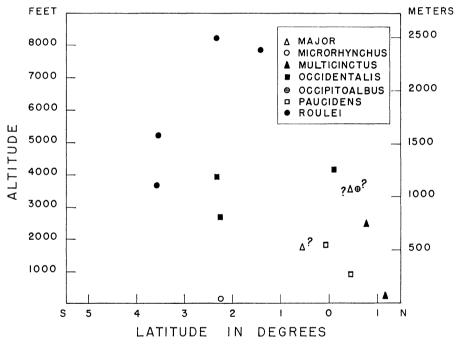


FIG. 10. Altitudinal and latitudinal distribution of *Atractus* in western Ecuador. See text for questionable records.

Any attempt to relate geographic distribution to the general problem of phylogeny is made difficult because of the great physiographic diversity of Ecuador. Figures 6–9 indicate the known locality records for all species in the Republic. However, because of the relatively short linear distances from north to south and east to west, associated with the abrupt and marked altitudinal changes across the Andean cordillera, these maps create an erroneous idea of proximity between the ranges of various forms. For example, one species may occur within a few linear miles of another, but the two may be separated from each other by several thousand feet of altitude. Unless due consideration is given to this physiographic barrier totally unwarranted assumptions concerning relationships might ensue. As an attempt to overcome this difficulty, Figures 10 and 11 have been prepared. These diagrams plot the known locality records of all Ecuadorian forms according to the latitude and altitude. The result is to emphasize the marked differences in vertical range for the various species and to indicate the degree of actual allopatry and sympatry among them. Figure 10 demonstrates the value of the method by clearly showing that the five species in

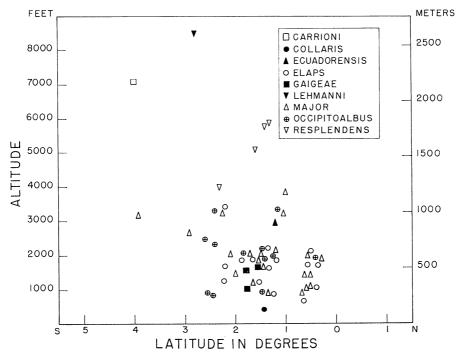


FIG. 11. Altitudinal and latitudinal distribution of Atractus in eastern Ecuador.

western Ecuador are allopatric, if the questionable records of A. major and A. occipitoalbus are ignored.

Figure 11 deals with the nine species of *Atractus* known from eastern Ecuador. The high montane species, *carrioni* and *lehmanni*, as well as the lower slope form, *resplendens*, are obviously allopatric populations. *Atractus elaps*, *gaigeae*, *major*, and *occipitoalbus* are more or less sympatric through-

out their ranges in the Oriente lowland. A. ecuadorensis from a moderate altitude probably is sympatric with one or the other of the lowland forms mentioned above. A. collaris of extreme eastern Ecuador occurs sympatrically with elaps and a major-like form elsewhere in its range, but a similar relationship is not as yet known in Ecuador. A. collaris allopatrically replaces gaigeae below 1000 feet in the upper Amazon area of Perú and adjacent Brazil.

Within the Badius Group, as represented in Ecuador, Atractus major of eastern Ecuador and Atractus multicinctus from the forested lowlands of the coastal northwest are apparently closely allied. In addition to the features common to all members of the group these forms agree, or differ only slightly from one another, in all characters of scutellation, dentition, and proportions. The primary differences between them are the much larger size attained by major (up to 512 mm. in standard length in males, up to 852 mm. in females, versus males to 300 mm. and females to 354 mm. in multicinctus) and details of the color pattern (major usually blotched, multicinctus always banded). Although the overlap in longitudinal counts (ventrals plus caudals, 188-221 in major, 208-226 in multicinctus), dentition (five to seven maxillary teeth in major, five or six in multicinctus), and coloration (some major banded, all multicinctus banded) makes specific identification of some individuals difficult, it seems doubtful that there is any direct relationship between them. A. major appears to be most closely allied to a series of populations ranging over most of the upper Amazon Valley; A. multicinctus ranges northward into Colombia and is probably related to other species of Atractus there.

Atractus modestus is superficially distinct from either of the other two Ecuadorian members of the Badius Group in having a uniform dorsal coloration and nine maxillary teeth. Although the only known specimen of the species has short loreals, approaching A. elaps in this respect, it seems probable (as indicated above under the species account) that this is an aberrant condition and that the population when rediscovered will prove to be characterized by long loreals. A. modestus agrees closely with major and multicinctus in all features except coloration and number of maxillary teeth. It is doubtful that modestus is directly allied to either of these latter species and its close relatives are probably to be sought outside the area of the present study.

The number of species belonging to the *Trilineatus* Group in Ecuador makes evaluation of possible relationships difficult. Those with 17 scale rows—A. collaris, dunni, ecuadorensis, gaigeae, lehmanni, microrhynchus, occidentalis, paucidens, and resplendens—differ from one another only in longitudinal scale counts and details of coloration. The three western species of this section-A. microrhynchus, occidentalis, and paucidens-are probably not directly related to the eastern forms. A. occidentalis does show some resemblance in coloration to ecuadorensis of the eastern Andean slope, but the two differ in dentition (maxillary teeth six or seven in the former, eight in the latter), ventral counts (in male occidentalis, 153, in females, 162; in male ecuadorensis, 144, probably about 154 in females), and hemipenial length (hemipenes to caudal, 18 in the former, 12 in the latter). A. occidentalis and paucidens appear to be closely related. They differ only in longitudinal scale counts (ventrals plus caudals, 188-192 in occidentalis, 200-223 in paucidens) and coloration (occidentalis with remnants of a dorsal pattern, paucidens uniform gray or brown dorsally). The allopatric distribution of the two forms, paucidens between 800 and 1600 feet (250-500 meters) along the lower slope of the Andes in northern Ecuador and occidentalis at slightly higher elevations, 2500 to 4000 feet (800-1200 meters) in the central part of the Andes, also supports the concept of close relationship between these species. It is possible that the two forms will ultimately be regarded as subspecifically related.

The inadequate original description of *A. microrhynchus* makes determination of its relationship impossible. If this form is actually from western Ecuador then its color pattern "like that of a *Tantilla*" suggests that it is a member of the *Trilineatus* Group. Most likely candidates as allies of *microrhynchus* would be occidentalis and paucidens, if this suggestion is supported by additional material.

The east Ecuadorian members of this group fall into two categories. First there are the extremely closely related forms *collaris* and *gaigeae* found in the lowland forest region. These two populations differ from one another only in longitudinal scale counts and coloration and are probably representatives of a single wide-ranging upper Amazon species. *A. collaris* is found in extreme eastern Ecuador and Amazonian Perú. *A. gaigeae* occurs over most of the Oriente region of Ecuador below 2000 feet (600 meters). The two forms agree with one another and differ from the other members of the *Trilineatus* Group from eastern Ecuador, with 17 scale rows, in their high longitudinal counts (ventrals plus caudals, 194–196 in *collaris*, 222– 240 in *gaigeae*; 164–185 in similarly colored species) and few maxillary teeth (five or six in the lowland forms, seven or eight in the other species).

A second series of forms-A. dunni, ecuadorensis, lehmanni, and resplendens-obviously related to collaris and gaigeae, is found in one interandean hoyo and at higher elevations along the east slope of the Andes. A. ecuadorensis and lehmanni are from the central Andes, the former from the Cordillera de Llanganate, Tungurahua Province, and the latter from the Hoyo de Cuenca, Azuay Province. A. dunni is known merely from "Ecuador," but its close approach to *ecuadorensis* and *lehmanni* suggests that it, too, is probably from the east Andean slope. The primary points of difference and similarity between the six east Ecuadorian species of this section are summarized in Table VII.

The three species, dunni, lehmanni, and ecuadorensis, may be arranged in that order on the basis of increasing longitudinal scale counts. A. dunni and lehmanni differ only slightly in ventral and caudal numbers and in the ventral plus caudal totals. A. ecuadorensis is similar to the other two forms in ventral counts, but has an unusually high number of caudals (41 in male holotype versus 25-28 in lehmanni and an estimated 30 in male dunni). The three forms may also be arranged in order on the basis of color pattern from ecuadorensis, with a nearly complete series of longitudinal dark stripes, through dunni, with the dorsolateral stripes broken up into discrete blotches and the lateral stripes discontinuous, to lehmanni, in which the pattern has been completely suffused with dark pigment to produce a uniformly colored dorsal pattern. A. dunni is more primitive than ecuadorensis in having most of the longitudinal stripes complete and in retaining a vertebral stripe. On the basis of coloration it appears that ecuadorensis is more closely related to dunni than to any other form. A. dunni and lehmanni agree in scutellation, but differ markedly in coloration. However, both of these forms are easily distinguished from ecuadorensis by having much lower caudal counts. Thus, dunni is visualized as being somewhat intermediate between the striped ecuadorensis and the uniform lehmanni, but it seems most closely allied to the latter form.

Atractus ecuadorensis approaches gaigeae to some extent as evidenced by its coloration and high caudal count. Further investigation may provide proof of intergradation between the highland population and gaigeae which occupies the lowland area just to the east of the type locality of ecuadorensis. A. dunni and lehmanni may also intergrade with one another, with ecuadorensis, or with gaigeae, although it is doubtful that the high altitude form lehmanni is in contact with either of the latter two species. It seems best at this time to retain all of these forms as distinct species although it is recognized that they are all closely related and probably there is some gene exchange between several of the populations. If a maximum amount of intergradation is postulated it might be predicted that the following relationships will ultimately be demonstrated (intergradation indicated by a dash): collaris-gaigeae-ecuadorensis-dunni-lehmanni.

Atractus resplendens has 17 scale rows and a uniform dorsum. It is found at altitudes between 3500 and 6200 feet (1100–1900 meters) in the eastern Andes of Ecuador. It differs from the striped members of the *Trilin*eatus Group having 17 scale rows in the low caudal count (25–31 in males,

REVISION OF Atractus

TABLE VII

CHARACTERISTICS OF EAST ECUADORIAN MEMBERS OF THE Trilineatus GROUP

Species	Ventrals		Caudals		Ventrals Plus	Maxillary		Color Pattern
	Males	Females	Males	Females	Caudals	Teeth		
Lowland collaris	163	175	31	21	194–196	5	Six continuous long- itudinal dark stripes and a paired series of regularly arrang- ed dark dorsolateral blotches; no verte- bral stripe.	
gaigeae Montane	187–198	207–213	35–39	25–27	222–240	5–6	tudii a pa dorse blote	n dark longi- nal stripes and aired series of blateral dark ches; a verte- stripe.
dunni		144		20	164		dark paire dorse blote dark s t r i	e longitudinal stripes and a ed series of olateral dark hes; a vertebral stripe; lateral pes partially en up into dark.
ecuadoren	144 sis 144		41		185	8	dark more tinuc terov no blotc dorso	ongitudinal stripes, all or less discon- ous except la- entral stripes; dorsolateral hes, but paired dateral stripes; ertebral stripe.
lehmanni	141–144	148–153	25–28	20–21	168–173	8	Dorsı dark scur	um a uniform brown, an ob- e vertebral e evident.
resplen- dens	157–174	170–185	25-31	14–19	182-203	7		um a uniform brown.

14-19 in females, versus 31-39 in males and 20-27 in females). It differs from lehmanni, a uniformly colored species (caudals in males, 25-28, in females, 20-21), in its much higher ventral counts (resplendens males, 157-174, females 170-185; lehmanni males, 141-144, females 148-153). In addition, resplendens is distinctive in usually having eight supralabials (77 per cent) and one postocular (86 per cent). The other Amazonian slope species of this section having 17 scale rows usually have seven supralabials and consistently two postoculars. Among these species, resplendens approaches gaigeae most closely in scutellation and lehmanni in coloration. The occurrence of melanism in this segment of the genus appears to be quite common and seems to have resulted in parallel evolution in color pattern between distantly related forms. For this reason the similarity in pattern between resplendens and lehmanni is regarded as being less significant than the resemblances in scutellation between the former and gaigeae. Whether resplendens and gaigeae are subpopulations of a single species cannot be determined at present. However, in view of the marked differences between them and the distribution of resplendens at elevations 2500 feet higher than those occupied by gaigeae, it seems doubtful that any direct contact between the two will be discovered. It is possible that resplendens and gaigeae may be connected through some other member of this stock found at an intermediate altitude. In this regard it may be noted that in this general division of the genus both melanistic members, resplendens and lehmanni, are from high altitudes.

The species of the Trilineatus Group with 15 scale rows also fall into two subdivisions. Atractus occipitoalbus is an eastern Ecuador species extremely close to the 17-scale-row forms in every respect but for the number of dorsal scale rows. The species exhibits a wide range of color variation from striped individuals resembling collaris and gaigeae, through melanistic examples still showing the striped pattern, to uniformly colored snakes similar to lehmanni and resplendens. A. occipitoalbus probably co-exists with gaigeae over part of its range in the lowlands of the Oriente, but the two forms differ in longitudinal counts (occipitoalbus ventrals plus caudals, 158-187, gaigeae, 222-240). Actually, occipitoalbus is more like resplendens than any striped form. The two species have seven maxillary teeth (sometimes eight in occipitoalbus), similar caudal counts (occipitoalbus males, 21-32, females, 9-19; resplendens males, 25-31, females, 14-19), and a considerable segment of the population has eight supralabials. In addition to the dorsal scale rows the two forms differ primarily in ventral counts (occipitoalbus males, 137-153, females, 150-171; resplendens males, 157-174, females, 170-185) and the occurrence of striped individuals in the occipitoalbus population.

The other two Ecuadorian trilineatus-like snakes with 15 scale rows do not appear to be closely related to occipitoalbus or to any of the 17-scalerow forms. These species, carrioni and roulei, are unique in consistently having six supralabials, one postocular, and a uniform color pattern without a suggestion of a light nuchal collar. From occipitoalbus they differ in the characters just listed, and, in addition, carrioni has no loreal shield and roulei has 10 or 11 maxillary teeth (occipitoalbus has a loreal and seven or eight maxillary teeth). While it is not improbable that the three species with 15 scale rows are related, the obvious relationships of occipitoalbus are with those with 17 scale rows. A. carrioni and roulei do not exhibit this approach to known species with 17 scale rows, and their affinities remain obscure. Inasmuch as there are few types with 15 scale rows, not only in Ecuador but throughout the range of the genus, and these have a discontinous distribution among species with 17 rows, it seems likely that the species with 15 scale rows have evolved as independent derivatives of forms

Character	carrioni	roulei	
Maxillary teeth	8–9	10–11	
Loreal	absent	present	
Ventrals:			
Males	145-149	140–145	
Females	152-159	145-149	
Caudals:			
Males	29-34	20-26	
Females	21–27	14-23	
Ventrals plus caudals	174-179	160-174	

TABLE VIII					
COMPARISON OF TWO SPECIES OF Atractus					

with 17 scale rows on several occassions. If this is so the relationships of *carrioni* and *roulei* may be sought most appropriately among the species with 17 scale rows. Among Ecuadorian species the most likely allies of these two are *lehmanni* and *resplendens*. However, any relationship to these latter forms must be rather a distant one.

A. carrioni and roulei are very much alike, the principal differences between them are in Table VIII.

A. carrioni is found in the Loja region of the Amazon drainage of southeastern Ecuador. A. roulei occurs along the western slopes of the central and southern Ecuadorian Andes. If the ranges of the two are actually

disjunct the separation must have been a recent one. Future collecting may reveal that the two species are still in contact through some of the low passes in southern Ecuador and constitute interbreeding geographic races. Both are known from fairly high altitudes, *carrioni* up to 7000 feet (2100 meters) and *roulei* to 8600 feet (2600 meters), so that this possibility is not unlikely.

The red and black ringed species, *Atractus elaps*, has 15 scale rows, an eastern distribution, and is not closely allied to any other Ecuadorian form. The only other known member of the *Elaps* Group is the red and black ringed species, *latifrons*, which replaces *elaps* at lower elevations in the Amazon Valley, but is not recorded from Ecuador. *A. elaps* and *latifrons* co-exist along the periphery of their ranges and do not appear to interbreed. Preliminary studies indicate that the two species can be distinguished from one another on the basis of average differences in segmental counts, but no difficulty is ever encountered in identifying them since *latifrons* has 17 dorsal scale rows and *elaps* 15.

CHECKLIST OF THE NOMINAL SPECIES OF ATRACTUS

The following list includes all described forms known to be based upon examples of the genus *Atractus*. Since no attempt has been made to analyze the status of non-Ecuadorian species, a considerable number of obvious and probable synonyms are listed. An asterisk (*) has been placed before all names reduced to synonymy in the present paper.

Each name is presented in its original form followed by a citation of the original description and the type locality. The names are arranged alphabetically.

- 1. Atractus andinus Prado. Ciencia (México), 1944, 5 (4/5): 111. Andes of Colombia.
- 2. Atractus arangoi Prado. Mem. Inst. Butantan, 1939, 13: 15. Colombia.
- 3. Calamaria badia Schlegel. Physionomie Serpens, 1837, 2: 35. Cayenne (French Guiana).
- Atractus balzani Boulenger. Ann. Mus. Civ. Storia Nat. Genova, 1898, (2) 19: 129. Missiones Mosetenes, northwest Bolivia.
- 5. *Atractus biseriatus* Prado. Mem. Inst. Butantan, 1940, 14: 26. Manizales, Departamento de Caldas, Colombia; Villamaria, Departamento de Caldas, according to E. R. Dunn.
- 6. *Atractus bocki* Werner. Mitt. Hamburg Mus., 1909, 26: 228. Cochabamba, Departamento de Cochabamba, Bolivia.
- 7. Atractus bocourti Boulenger. Cat. Snakes British Mus., 1894, 2: 306. Acomayo, Departamento de Huanuco, Perú.
- 8. Atractus boettgeri Boulenger. Cat. Snakes British Mus., 1896, 3: 645. Yungas, Sierra de las Yungas, Departamento de Cochabamba, Bolivia.
- 9. Atractus boulengeri Peracca. Bol. Mus. Zool. Anat. Comp. Torino, 1896, 11 (252): 1. South America.
- 10. *Rhabdosoma brevifrenum Jan = A. elaps. Prodromo ofidi, 1862, 1: 12. Brasil.
- 11. Atractus carrioni Parker. Ann. Mag. Nat. Hist., 1930, (10) 5: 207. Loja, Provencia de Loja, Ecuador.

- 12. Atractus clarki Dunn and Bailey. Bull. Mus. Comp. Zool., 1939, 86 (1): 8. Mine at Santa Cruz de Cana, Provencia de Darién, Panamá.
- 13. Atractus collaris Peracca. Bol. Mus. Zool. Anat. Comp. Torino, 1897, 12 (284): 4. Río Cononaco, Provencia de Napo-Pastaza, Ecuador.
- 14. Atractus colombianus Prado. Mem. Inst. Butantan, 1939, 13: 18. Chocontá, Departamento de Cundiamaraca, Colombia.
- 15. Rhabdosoma crassicaudatum C. Duméril, Bibron, and A. Duméril. Erpétologie Gén., 1854, 7 (1): 103. Bogotá, Departamento de Cundinamaraca, Colombia.
- *Geophis diplozeugus Schmidt and Walker = A. elaps. Chicago Nat. Hist. Mus., Zool. Ser., 1943, 24 (26): 286. Departamento de Madre de Dios, Perú.
- 17. Rhabdosoma dubium Jan. Prodromo ofidi, 1862, 1: 18. Bogotá, Departamento de Cundinamaraca, Colombia.
- 18. *Atractus duboisi Boulenger = A. occipitoalbus. Bull. Soc. Zool. France, 1880: 44. Andes of Ecuador.
- 19. Atractus dunni Savage. Proc. Biol. Soc. Washington, 1955, 68: 14. Ecuador.
- 20. Atractus ecuadorensis Savage. Proc. Biol. Soc. Washington, 1955, 68: 15. Llangate area; probably Cordillera de Llanganate, Provencia de Tungurahua, Ecuador.
- 21. Rhabdosoma elaps Günther. Cat. Colub. Snakes British Mus., 1858: 241. Guayaquil, Provencia de Guayas, Ecuador; in error.
- 22. Geophis emmeli Boettger. Ber. Senckenberg Gesells., 1888: 192. Río Mapiri, Departamento de La Paz, Bolivia.
- 23. Atractus erythromelas Boulenger. Ann. Mag. Nat. Hist., 1903, (7) 11: 483. Merída, Estado de Merida, Venezuela.
- 24. Atractus fuhrmanni Peracca. Mem. Soc. Neuchatel, 1914, 5: 100. Bogotá, Departamento de Cundinamaraca, Colombia.
- 25. Coluber fuliginosa Hallowell. Proc. Acad. Nat. Sci. Philadelphia, 1845: 243. Caracas, Distrito Federal, Venezuela.
- 26. Atractus gaigeae Savage. Proc. Biol. Soc. Washington, 1955, 68: 12. Provencia de Santiago-Zamora, Ecuador.
- 27. Atractus guentheri Wucherer. Proc. Zool. Soc. London, 1861: 115. Cannavieiras, south of Bahia (São Salvador), Estado do Bahia, Brasil.
- 28. Elaps herthae Ahl. Zool. Anz., 1927, 70 (9/10): 252. Mundurucú, Río Manacapurú, Estado do Amazonas, Brasil.
- 29. Atractus indistinctus Prado. Mem. Inst. Butantan, 1939, 13: 16. Ocaña, Departamento de Norte de Santander, Colombia.
- Atractus iridescens Peracca. Bol. Mus. Zool. Anat. Comp. Torino, 1896, 11 (252): 2. South America.
- 31. Atractus lasallei do Amaral. Bull. Antivenin Inst., 1931, 4(4): 87. Sampedro, south of Medellín, Departamento de Antioquia, Colombia.
- 32. Geophis latifrons Günther. Ann. Mag. Nat. Hist., 1868, (4) 1: 415. Pébas, Departamento de Loreto, Perú.
- 33. Atractus lehmanni Boettger. Katal. Rept. Mus. Senckenberg, 1898, 2: 80. Cuenca, Provencia de Azuay, Ecuador.
- 34. Leptocalamus limitaneus do Amaral. Mem. Inst. Butantan, 1935, 9: 219. La Pedrera, Río Caquetá, Comisaria de Amazonas, Colombia.
- 35. Atractus longimaculatus Prado. Mem. Inst. Butantan, 1939, 13: 17. Nevada Quindío, Departamento de Caldas, Colombia; in error for Pacho, Departamento de Cundinamaraca, Colombia, according to E. R. Dunn.
- 36. Atractus loveridgei do Amaral. Bull. Antivenin Inst., 1930, 4 (2): 28. Jericó, Departamento de Antioquia, Colombia.

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- 37. Isoscelis maculata Günther. Cat. Colubr. Snakes British Mus., 1858: 204. Unknown.
- 38. *Rhabdosoma maculatum Bocourt = A. dunni. Miss. Sci. Mexique, 1883, 540. Ecuador.
- 39. Atractus major Boulenger. Cat. Snakes British Mus., 1894, 2: 307. Canelos, Provencia de Napo-Pastaza, Ecuador.
- 40. Atractus manizalensis Prado. Mem. Inst. Butantan, 1939, 13: 17. Colombia (paratype from Manizales, Departamento de Caldas, Colombia); both specimens from Villamaria, Departamento de Caldas, according to E. R. Dunn.
- 41. Atractus melanogaster Werner. Zool. Anz., 1916, 47 (11): 309. Cañon del Tolima, Departamento de Tolima, Colombia.
- 42. Atractus melas Boulenger. Ann. Mag. Nat. Hist., 1908, (8) 1: 114. Los Mangos = Los Cisneros = Juntas, Departamento Valles, Colombia.
- 43. Rhabdosoma microrhynchum Cope. Proc. Acad. Nat. Sci. Philadelphia, 1868: 102. Guayaquil, Provencia de Guayas, Ecuador.
- 44. Atractus micheli Mocquard. Bull. Mus. Hist. Nat., Paris, 1904, 10 (6): 301. French Guiana.
- 45. Atractus modestus Boulenger. Cat. Snakes British Mus., 1894, 2: 304. Western Ecuador.
- 46. Rhabdosoma badium multicinctum Jan (in Jan and Sordelli). Icon. Ophidiens, 1865, 10: Pl. 4, Fig. 5. Lima, Departamento de Lima, Perú; apparently in error.
- 47. Atractus nicefori do Amaral. Bull. Antivenin Inst., 1930, 4 (2): 28. Jericó, Departamento de Antioquia, Colombia.
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- 55. Atractus pamplonensis do Amaral. Congress Internat. Zool., Lisbon, 1937; 1763. Pamplona, Departamento de Norte de Santander, Colombia.
- 56. Atractus paraguayensis Werner. Sitz. Akad. Wiss., Wien, 1924, 133 (1): 40. Paraguay.
- 57. Atractus paucidens Despax. Bull. Mus. Hist., Paris, 1910, 16 (7): 372 Santo Domingo de los Colorados, Provencia de Pichincha, Ecaudor.
- Atractus pauciscutatus Schmidt and Walker. Chicago Nat. Hist. Mus., Zool. Ser., 1943, 24 (28): 362. Carpapata, upper Chanchamayo Valley, northeast of Tarma, Departamento de Junín, Perú.
- 59. Rhabdosoma peruvianus Jan. Prodromo ofidi, 1862, 1: 12. Perú.
- 60. *Rhabdosoma pöppigi Jan = A. elaps. Prodromo, ofidi, 1862, 1: 11. Brasil.
- 61. Atractus punctiventris do Amaral. Mem. Inst. Butantan, 1932, 7: 117. Villavicencio, Intendencia de Meta, Colombia.
- 62. Rhabdosoma punctovittatum Jan. Prodromo ofidi, 1862, 1: 17. Antille.
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- 66. Rhabdosoma badium rubinianum Fillippi (in Jan). Prodromo ofidi, 1862, 1: 14. Venezuela.
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- 69. Atractus serranus do Amaral. Bull. Antivenin Inst., 1930, 4 (3): 65. Serra de Paranapiacaba, Estado do São Paulo, Brasil.
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- 75. Atractus trilineatus Wagler. Isis von Oken, 1828, 21: 742. South America.
- 76. Rhabdosoma trivirgatum Jan. Prodromo ofidi, 1862, 1: 17. Unknown.
- 77. Atractus trivittatus do Amaral. Mem. Inst. Butantan, 1932, 7: 118. Chita, Departamento de Santander, Colombia.
- 78. Rhabdosoma univittatum Jan. Prodromo ofidi, 1862, 1: 15. Caracas, Distrito Federal, Venezuela.
- 79. Atractus variegatus Prado. Mem. Inst. Butantan, 1941, 15: 379. La Uvita, Departamento de Boyacá, Colombia.
- 80. Rhabdosoma varium Jan. Prodromo ofidi, 1862, 1: 18. Santa Cruz de la Sierra, Departamento de Santa Cruz, Bolivia.
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- 84. *Atractus wagleri* Prado. Ciencia (Mexico), 1945, 6 (2): 61. Humbo, Departamento de Boyacá, Colombia.
- 85. Atractus werneri Peracca. Mem. Soc. Nuechatel, 1914, 5: 102. Near Viotá, Departamento de Cundinamaraca, Colombia.
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Accepted for publication August 1, 1958



