STUDIES ON AMPHISBAENIDS (AMPHISBAENIA, REPTILIA)

3. THE SMALL SPECIES FROM SOUTHERN SOUTH AMERICA COMMONLY IDENTIFIED AS *AMPHISBAENA DARWINI*

CARL GANS

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 134 : ARTICLE 3 NEW YORK : 1966

STUDIES ON AMPHISBAENIDS (AMPHISBAENIA, REPTILIA)

•

3. *THE SMALL SPECIES FROM SOUTHERN SOUTH AMERICA COMMONLY IDENTIFIED AS* AMPHISBAENA DARWINI

CARL GANS

Research Associate, Department of Herpetology
The American Museum of Natural History
Professor of Biology
State University of New York at Buffalo

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 134 : ARTICLE 3 NEW YORK : 1966

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 134, article 3, pages 185–260, text figures 1–45,
plates 37–45, tables 1–3

Issued December 10, 1966

Price: $4.00 a copy

CONTENTS

INTRODUCTION

THE ABSENCE UNTIL VERY RECENTLY of any revisionary work on the South American species of amphisbaenids has produced some peculiar assemblages. Perhaps the most complex of these includes a wide-ranging group of forms with approximately 200 body annuli, generally fewer than 40 segments to a mid-body annulus, and four precloacal pores. Approximately eight names are based on samples of this group. The concepts associated with these are very unclear. More than 10 per cent of the museum specimens assignable to the composite assemblage bear still other names, and the majority of the remainder appear to have been identified as *Amphisbaena darwini* Duméril and Bibron.

A survey of the Amphisbaenia in museum and university collections indicated that there was a very large sample (more than 700 specimens) of the present group available for study. A review of the sample showed both a marked geographic variation and a peculiar local dimorphism in parts of the range. The routine counts ordinarily used for species discrimination (see earlier papers) did not separate the forms.

Only when additional characteristics were included in a "non-dimensional species" analysis was it possible to show that two widely sympatric, yet superficially very similar, species groups were being sampled. The subject of the present paper is the characterization and a discussion of these groups. Several other small forms from the same region but possibly pertaining to different groupings are also characterized. This paper also presents additional comments on the utility of the various characteristics used in species differentiation.

Since this analysis is of necessity a first-level one, I omit all but the most superficial discussion of ecological factors. I am postponing zoogeography and statements regarding the relation of forms and the generic pattern until all the species have been characterized. The limitations and, I hope, the utility of the approach are obvious; they have been discussed in previous papers of the series.

Although the number of specimens here discussed is much larger than that available to earlier workers, it is unfortunately still inadequate. Situations such as that in Rio Grande do Sul involve the presentation of hypotheses with a high degree of uncertainty. Representation of the states of central and western Argentina, of Santa Catarina, Paraná, inland Rio Grande do Sul, southern Mato Grosso and Minas Gerais in Brazil, indeed of almost all the range, is as yet too sketchy. A concerted program of collecting remains as the prerequisite for settling the outstanding issues.

The present paper is designed to make this subsequent work as simple as possible by the citation of detailed specimen and literature records, and by a step-by step presentation of the analysis. I have omitted literature records unless the specimens were at hand or the description left no doubts as to identification. The references to anatomical information are given with some hesitation, because the identifications used by previous workers bear little resemblance to the names proposed here. The papers refer to the group as a whole, and even then it is necessary to consider the possibility that small specimens of *Amphisbaena angustifrons*, *A. camura*, *A. dubia*, *A. mertensi*, *A. vermicularis*, and similar forms may have been used. I believe, however, that the importance of citing these outweighs the uncertainty of specimen identification.

It is a pleasure to acknowledge the assistance of friends and colleagues, particularly in South America, who lent or presented me with specimens, provided maps and locality data, and helped me see living animals in the field. The field work was greatly facilitated by Messrs. Werner C. A. Bokermann, Silvio Mendes Corrêa, Celso P. Jaeger, Miguel A. Klappenbach, Braulio Orejas-Miranda, and A. S. F. Ditadi. The specimens cited came from the following collections (identified by abbreviations throughout the text):

A.M.N.H., the American Museum of Natural History (C. M. Bogert and R. G. Zweifel)

A.N.S.P. Academy of Natural Sciences of Philadelphia, Pennsylvania (J. Böhlke and E. V. Malnate)

B.M., British Museum (Natural History), London

(J. C. Battersby and A. G. C. Grandison)
B.Y.U., Brigham Young University, Provo, Utah (W. W. Tanner)
C.A.S., the California Academy of Sciences, San Francisco, California (A. E. Leviton)
C.G., Carl Gans, private collection
C.M., Carnegie Museum, Pittsburgh, Pennsylvania (N. D. Richmond)
C.N.H.M., Chicago Natural History Museum, Chicago, Illinois, now Field Museum of Natural History (R. F. Inger and H. Marx)
D.Z., Departamento de Zoologia, Secretaria da Agricultara, São Paulo, São Paulo, Brazil (P. E. Vanzolini). This collection now includes all lizards formerly in the Instituto Butantan of São Paulo
H.M., Zoologisches Museum, Hamburg, Germany (all types destroyed) (W. Ladiges)
H.U.J., Hebrew University, Jerusalem, Israel (G. Haas)
I.B.M., Instituto de Biología, Mendoza, Argentina (J. M. Cei)
I.M.L., Instituto Miguel Lillo, San Miguel de Tucuman, Argentina (K. Hayward and R. F. Laurent)
I.M.Z.U.T., Istituto e Museo di Zoologia della Universitá di Torino, Italy (L. Pardi and L. Rossi)
I.N.M., Instituto Nacional Malbran, Buenos Aires, Argentina (A. Barrio)
K.M., Universitetets Zoologiske Museum, Copenhagen, Denmark (F. W. Braestrup)
L.I.H.U.B.A., Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina (O. A. Reig)
M.A.C.N., Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (J. Cranwell and J. M. Gallardo)
M.C.S.N., Museo Civico di Storia Naturale, Verona, Italy (Ruffo)
M.G., Museum de Genève, Switzerland (V. Aellen)
M.H.N.P., Museum National d'Histoire Naturelle, Paris, France (J. Guibé)
M.N., Museo Nacional, Rio de Janeiro, Guanabara, Brazil (A. L. de Carvalho)
M.N.H.M., Museo de Historia Natural de Montevideo, Uruguay (M. A. Klappenbach and B. Orejas-Miranda)
M.R.C.N., Museu Rio-Grandense de Ciências Naturais, Pôrto Alegre, Rio Grande do Sul, Brazil (T. de Lema)
M.S.N.G., Museo Civico di Storia Naturale "Giacomo Doria," Genoa, Italy (E. Tortonese and L. O. Capocaccia)
N.H.M.B., Naturhistorisches Museum, Bern, Switzerland (H. Sägesser)
N.M.B., Naturhistorisches Museum, Basel, Switzerland (L. Forcart)
N.M.W., Naturhistorisches Museum zu Wien, Vienna, Austria (J. Eiselt)
P.U.M., Universitá di Pisa, Italy (M. Benazzi)
R.M.N.H., Rijksmuseum vor Naturlijke Historie, Leiden, the Netherlands (M. Boeseman)
S.M.F., Senckenbergische naturforschende Gesellschaft, Frankfurt-am-Main, Germany (K. Klemmer)
S.M.N.S., Staatliches Museum für Naturkunde, Stuttgart, Germany (H. Wermuth)
U.M.M.Z., University of Michigan Museum of Zoology, Ann Arbor (C. F. Walker)
U.R.G.S., Instituto de Ciências Naturais, Universidade de Rio Grande do Sul, Pôrto Alegre, Rio Grande do Sul, Brazil (C. P. Jaeger and S. Mendes Corrêa)
U.S.N.M., United States National Museum, Smithsonian Institution, Washington, D. C. (D. Cochran)
Z.I.L., Zoological Institute, Academy of Sciences, Leningrad, U.S.S.R. (Ilja S. Darevski)
Z.M.U., Zoologisches Museum der Universität, Berlin, Germany (H. Wermuth and G. Peters)
Z.S.M., Zoologische Sammlung des Bayerischen Staates, Munich, Germany (W. Hellmich)
Z.V.C.-R., Departamento de Zoologia Vertebrados, Facultad de Humanidades y Ciencias, Universidad do Montevideo, Uruguay (R. Vaz-Ferreira)

It was necessary to return all the British Museum material before this study was completed. Some of the São Paulo museum specimens (notably the type series) were examined in Brazil in 1963; they too were unavailable for the final review.

I am particularly grateful to Drs. Antenor L. de Carvalho and Oswaldo A. Reig and Mr. Werner C. A. Bokermann for the gift of numerous maps and atlases, which facilitated the assignment of localities.

Mr. Mark Amdur spent considerable effort checking these analyses. Mr. Herbert Rosenberg, Mr. Robin Moest, and the Misses Claudia Guerin and Kathy Horton furnished technical assistance. Dr. Virginia Cummings rendered the drawings.

This series of studies has been supported by grants G-21819 and GB-2460 from the National Science Foundation.

PROCEDURES

Localities

Figures 1 and 2 show the various sites mentioned in the text. They have been located on the basis of available maps and atlases and plotted in approximate positions. The sketch maps thus serve mainly to define the relative positions of sites; the scale is obviously too great to permit absolute accuracy of placement.

I have accepted the information given on the specimen labels with few exceptions, but reservations regarding their accuracy remain. For example, there are a few specimens of *A. darwini* from "Misiones," but none from the states of Corrientes and Entre Rios. Since the labels of the former refer to the state only, one might question the occurrence of this form in northeastern Argentina. The paucity of records for other species of amphisbaenians, indeed for other Squamates, suggests that it is more useful to cite such records even though with reservations.

Characters

The methods of measurement and counting generally follow the procedures described by Gans and Alexander (1962), because various subsequent, still unpublished studies have indicated the usefulness of their general approach. The data for these characters have been deposited as Document Number 8998 with the ADI Auxiliary Publication Service, Library of Congress, Washington 25, D. C. A copy may be secured by citing the Document Number and by remitting $6.25 for photoprints, or $2.50 for 35-mm. microfilm. Advance payment is required. Make checks or money orders payable to: Chief, Photoduplication Service, Library of Congress.

The forms discussed may be separated by various patterns of head shape, segment proportions, and similar characteristics. I have emphasized meristic characters, as these are easier to describe. Furthermore, their nature is easier to communicate to workers who may not wish to become deeply involved in amphisbaenid segmental geometry and nomenclature.

Annuli and Segments: All counts of body annuli were made along the left side of the ventral surface from the first postoral annulus up to and including the annulus bearing the precloacal pores. Irregularities were recorded.

Alexander's study (1966) of dermal-vertebral correlations in *Blanus* has recently confirmed the fact that a relatively constant number of anterior body annuli extends across the posterior portion of the skull, and that the position of the cloaca shows essentially minor variation relative to the trunk-caudal and vertebral transition. The variability and number of body annuli, then, reflect only the number of intercalated half-annuli (which may be determined by inspection) and the variability of the vertebral column. Subsequent studies (Alexander and Gans, 1966) have confirmed this fact for specimens sampled from the present series. The dermal-vertebral correlation is constantly better on the ventral than on the dorsal surface, which indicates that the additional dorsal half-annuli are truly intercalated.

Caudal annuli were counted from the first complete (ventrally not reduced) postcloacal up to and including the last complete annulus showing regular segments. The half-annuli, dorsal and lateral to the patch of modified cloacal scales, are referred to as lateral. The position of the reduced and possibly narrowed autotomy annulus, or annuli, immediately before or after which autotomy may take place, is recorded as a number (counting from the cloaca). In the tables of raw data available from the ADI Auxiliary Publications Project (see above), these values are given as body plus lateral plus (autotomy) caudal annuli, i.e., 213+3+(7)19.

The segments of an annulus are irregular in number and relative shape, and they may vary among adjacent annuli. Counts of dorsal and ventral segments were made in the midbody region continuously around a single annulus selected at random, and were recorded as dorsals plus ventrals, i.e., 18+20. Whenever a check of the midbody area indicated variability in segment number (as well as proportion), additional counts were made of three or five adjacent annuli, and the ranges are given. The comparisons were of maximum, minimum, and median value

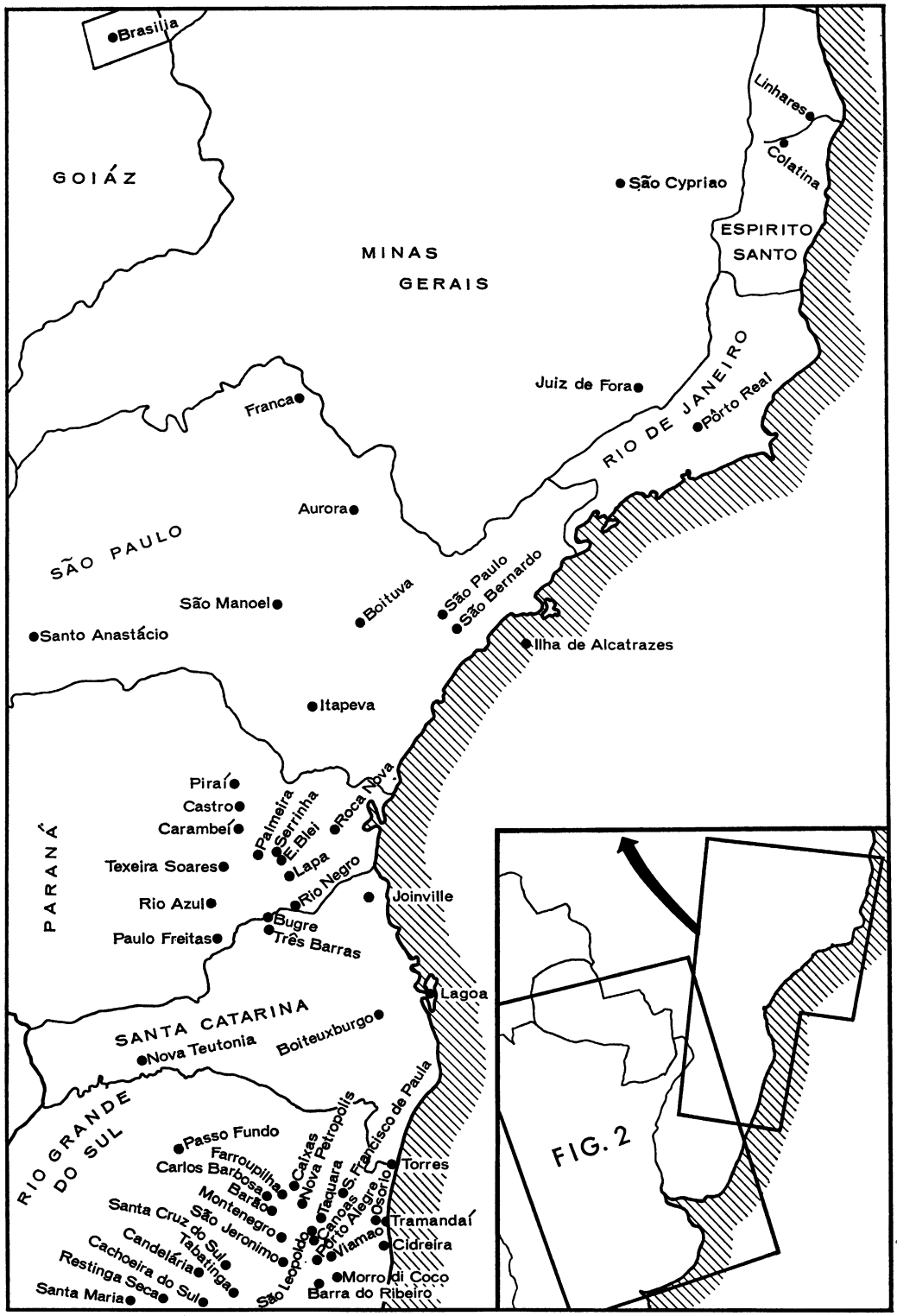


FIG. 1. *Amphisbaena*. Sketch map to show Brazilian localities mentioned in the text. The insert shows the southeastern quadrant of South America and the regions covered by the large-scale maps shown in figures 1 and 2.

FIG. 2. *Amphisbaena*. Sketch map of the localities in the southern portion of the range.

(range at midpoint). The median value was generally plotted in figures 8 and 24 and is given in table 1.

For certain discriminations the highest number of segments of any annulus at post-autotomy level was useful. The number of segments on at least four annuli was sampled on each specimen. Only the maximum value and the annulus on which it occurred were recorded. Only the value is given in the raw data, where it is tabulated as "Caudal Maximum Segments" for specimens of *Amphisbaena darwini*.

There was considerable, even intrapopulational, variability in segment proportions. The values given for these represent approximations to some sort of sample mean. Here, as in all of these studies, the assumption that the segment number is fixed at term, which is implicit in most taxonomic discussions of reptiles, has been accepted. Changes of means or ranges between samples drawn from juvenile and adult populations are assumed to be the result of the selection of juveniles. It might be interesting to check whether segmental, as opposed to annular, numbers are indeed fixed in the lifetime of a specimen.

HEAD SEGMENTATION: The concept (Gans and Alexander, 1962) that the head scalation represents an overlap between two fields of influence has proved very useful in subsequent descriptions of the cephalic segmentation. All forms here discussed show enlargement of the rostral, nasal, prefrontal, and frontal segments, of the three supralabials and three infralabials, and the mental, postmental,[1] and malar segments.

Unpublished functional studies confirm the fact that the enlargement pattern of these, as well as of the parietal, segments bears distinct correlations with the mode of locomotion. The cephalic segments undergo a series of complete and partial fusions and subdivisions. The relative constancy or variability of a region, rather than segmental geometry, thus has functional, and of course systematic, importance. In contrast it is difficult and probably trivial to establish homologies for this region, even within the amphisbaenians.

Striking individual variation exists in the position of the angulus oris. This fact is emphasized, because the postsupralabials and postinfralabials are relatively small and short segments. Minor changes in their arrangement and position cause a shift from a 3 (supralabial)+3 (infralabial) value to a $3+3\frac{1}{2}$, a $4+3$, or a $3\frac{1}{2}+3$ pattern. Many specimens were found to be asymmetrical, and the values have hence been omitted from the tables of raw data (see p. 191). These observations are of interest because most other species thus far studied show considerable constancy in the position of the angulus oris.

The nature of the parietal enlargement—or, rather, the relative sizes of the middorsal segments of the first and possibly the second trunk or intercalated dorsal half-annuli—proved to be very critical for the discrimination of certain species groups. The presence of parietals, larger than the preceding frontals, as well as the number of enlarged pairs are recorded in the raw data (see p. 191).

CLOACAL REGION: The number of precloacal pores has long been known as a remarkably useful means for initial discrimination. The present studies have confirmed this fact. This does not mean that there is no variation, but rather that the nature of the variation is again species specific. In the present series the range extends only plus or minus one (three to five) for more than 99 per cent of the available sample.

Some of the forms here characterized show marked sexual dimorphism in the shape and size of pores. Mature males exhibit solid secretion cores, whereas juveniles and females have the pores reduced to scar-like markings that lack any core. The frequency of pore scars, rather than cored pores, in some populations is sufficiently high to suggest seasonal variation of pore size in males. Some males also exhibit mixed rows, with one, two, or three positions showing pore scars, and three, two, or one positions with filled cores. Both the function and development of these structures might usefully be subjected to a separate study.

BODY PROPORTIONS: Snout-to-vent and tail

[1] Thomas (1965) recently and quite correctly pointed out that this segment should be called the genial. Etymological consistency rather than homology is involved (cf. Gans, 1960), and it would in this case force a confusing change in nomenclature. Ease of comparison by those persons who will use these papers appears more important, so I retain the present term.

measurements were read by adpressing the specimen to a meter stick. Body diameter was measured at the widest, undeformed site along the first third of the trunk. These animals utilize the lateral sulci as expansion joints, and the diameter hence shows some variation with different methods of fixation.

CAUDAL PROPORTIONS AND SEGMENT MODIFICATIONS: The proportions of the tail and the shape of the caudal tip appear to be diagnostic in the characterizing of amphisbaenids, i.e., they vary between species and are constant within populations. The only limitations are those relating to ontogenetic changes and the nutritional state of the animal. The tail contains a certain amount of adipose tissue, and well-fed specimens have relatively fatter, more turgid tails than do starving individuals. Laboratory observations indicate that the process is reversible. The proportions of the caudal tip do reflect the nature of the tissue connections between skin and caudal vertebrae; they are more or less recognizable even in shrunken specimens and were utilized in discrimination.

A variety of species in the genus *Amphisbaena* shows a distinctive caudal modification characterized by the fact that segments of the dorsolateral aspect of the caudal tip are produced and swollen into a series of tubercles (Gans, 1962, 1964b). This is also characteristic of one of the forms described in the present study, in which the sample is adequate to show that the expression of the tuberculation shows ontogenetic change. Hatchlings and juveniles lack the tuberculation, which is developed only in adults. Even the former specimens differ in having clearly inscribed interannular sutures expressed to the caudal tip, which is subdivided by a single vertical suture.

OTHER CHARACTERS: A few specimens were available for more destructive procedures. Some individuals had everted hemipenes. In each case, the samples were insufficient to assist in the initial discrimination of the species. The results of the comparisons, discussed elsewhere, serve mainly to check what may be the differences between the species groups defined by the present analysis. Where pertinent, the results have been mentioned in the discussion of the particular species.

ANALYSIS

DISCRIMINATION OF SPECIES: The genus *Amphisbaena* has not been reviewed during the last three-quarters of a century. The available synonymies (cf. Amaral, 1937) were based on analysis of inadequate samples. Furthermore, museum identification of specimens had long been in catch-all groupings that often mixed individuals belonging to diverse species and genera (cf. Vanzolini, 1949).

For these reasons my review of the genus was begun by my assembling a maximal number of specimens. Those forms of which the recognition, characterization, and synonymy posed the least problems were then separated out, and diagnoses and summaries of geographic variation were provided for them. This process allowed the separation of the various large and medium-sized forms with high numbers of segments to a midbody annulus as well as the various small forms characterized by distinct color patterns, body proportions, or segment and pore arrangements.

There remained a curious assemblage, mostly of specimens identified earlier as *Amphisbaena darwini* (although many individuals also identified as *darwini* had earlier been shown to belong to different species). The present sampling of this assemblage included specimens from the level of northern São Paulo (Brazil) southward along the eastern coastal regions of South America and inland through Uruguay and across Argentina. Also used were a few individuals from Minas Gerais, Rio de Janeiro, and Espirito Santo (Brazil), and from Paraguay and Bolivia.

Even preliminary inspection of the data indicated that some peripheral populations showed drastic differences from the main assemblage and presumably represented distinct forms. The vast majority of specimens and populations, however, resisted immediate sorting. They comprised an assemblage characterized by specimens with four precloacal pores, counts of nearly 200 body annuli and of generally fewer than 40 segments to a midbody annulus. The Brazilian material, in particular, exhibited dimorphism in color pattern and in tuberculation of the caudal segments—a dimorphism possibly

correlated with differences in absolute body size.

The possibility that two discrete, but sympatric, species were involved was particularly interesting in view of Klappenbach's (1960) description of a similar situation in southern Uruguay. The dimorphism also suggested additional problems, as the populations showing each color pattern demonstrated marked and non-parallel variation in numerous characters.

The situation thus represented an obvious case for the type of analytical approach detailed in an earlier study (Gans, 1959). The approach consists of a "non-dimensional species analysis," which may be defined as an initial separation of forms that behave as good species in the localities where they occur sympatrically. This is followed by the "recognition of species in space," or an examination of the relationships of the previously determined, discrete, and allopatric populations. The two tests of conspecificity at this level are a continuity of range and the existence of specimens intermediate in the characters in which the populations differ, particularly if these specimens were collected at intervening localities. The approach of the earlier study is followed in somewhat abbreviated fashion, with the omission of the comparisons that yielded negative results.

GEOGRAPHIC VARIATION: Previous papers (Gans, 1959, 1964a, 1965) have shown the development of a method for stating geographical variability. This method is designed to permit the rapid assignment of more recently collected specimens to populations and the testing and re-evaluation of the patterns presented. The format, which is followed here, consists of graphs and diagrams summarizing the major variational trends separately for each character, a minimum of text, and an appendix that presents the raw data in the most concise manner (see first paragraph under Characters, p. 191).

Subspecies have been recognized only in cases in which several characters, each otherwise constant, appeared to undergo a step change across a relatively narrow geographic zone. I have used a conservative approach in the naming of populations, since the specimens studied are often inadequate, and ecological data, very important in testing the observed patterns, are as yet unavailable.

THE RECOGNITION OF "NON-DIMENSIONAL" SPECIES

PROCEDURE

COLOR PATTERN and the presence or absence of caudal tuberculation were the characteristics that had initially suggested that the two populations were dimorphic.

Two discrete color patterns were noted. In the first, each segment was entirely and uniformly pigmented; the pigment dropped out by segments, in a checkerboard fashion, some variable distance below the lateral line. In the second, the segments were variably and non-uniformly marked, and the pigmentation faded out uniformly along the sides of the animal, either by a weakening of pigment density or by a diametric or areal reduction of the pigmented zone.

Both of these characters proved inadequate for an initial separation of samples. The color pattern was often too faded to permit decisions, while the caudal tuberculation varied ontogenetically. Comparison of well-preserved adults added several additional characteristics to the discrimination sequence. It also turned up the interesting observation that the specimens exhibiting variants of the "non-checkerboard" or "countershaded" pattern were themselves dimorphic in certain geographical sites.

A comparison of various characteristics suggested the utility of an initial breakdown based on multiple characteristics. The first category of this breakdown, called *low* for the sake of convenience, combined specimens that generally were of smaller adult size, and had low numbers of midbody (and maximum caudal) segments, checkerboard or countershaded coloration, enlarged parietals, and a smooth segmentation of the caudal tip. The second category, referred to as *high*, combined specimens that generally were of larger adult size, and had high numbers of midbody (and maximum caudal) segments, only countershaded coloration, small or undifferentiated parietals, and a tuberculation of the caudal tip.

The use of more than one characteristic in achieving the initial discrimination does not invalidate the scheme; it does require that the several discriminating characters also be tabulated.

THE SITUATION IN THE NORTHERN PORTION OF THE RANGE

The distribution of records along the northern portion of the sampled range (Espirito Santo, Minas Gerais, Rio de Janeiro, São Paulo, northern Paraná) is exceedingly curious. Specimens are available from a number of sites, yet most sites are represented by only one to three specimens. The largest single sample comes from the coastal island Ilha dos Alcatrazes. Only six specimens come from the city of São Paulo (possibly from its vicinity). This paucity of records is particularly significant, because the entire collection formerly in the Instituto Butantan was used, a collection that generally has good distributional representation from São Paulo.

A map (fig. 3) shows the distribution of *low* and *high* specimens. All northern records contain only *low* specimens, except for Aurora and São Manuel in central São Paulo, and the mixed sites of São Paulo, Piraí, and Santo Anastacio.

Inspection indicated that there was marked geographic variation among the isolated northern *low* samples. Comparisons of patterns is thus restricted to the actual sites of sympatry. The data for characters showing differences are given in table 1. In spite of the small number of available specimens, these show that the two forms compared are certainly distinct. They differ in the nature of the parietal segmentation and in caudal shape and segmental tuberculation. The total body size differs markedly, although both samples include adults. Differences also occur in the median numbers of dorsal and ventral segments to a midbody annulus, in the maximum number of segments around the tail, in the frequency of specimens lacking the postmalar row, and in the expression of the precloacal pores. Even female *low* specimens have large pores; all but fully adult males of *high* pattern have tiny pores or pore scars. The evidence from the number of caudal an-

FIG. 3. *Amphisbaena*. Localities for *low* (solid circles) and *high* (open circles) specimens in the northern portion of the range.

nuli is unclear. The *low* and *high* samples from São Paulo thus appear to have been sampled from two discrete species.

THE SITUATION IN PARANÁ AND SANTA CATARINA

Several extensive series are available from eastern Paraná. With the above-discussed exception of the Piraí sample, these are composed entirely of *high* specimens, as are the individuals from the northern fringe of Santa Catarina and the specimens from Lagoa.

Western Paraná and southern and western Santa Catarina lack representation. Collections include specimens from only three sites: Boiteuxburgo, Nova Teutonia (Santa Catarina), and Foz do Iguaçu. The last two have only *high* specimens. The pattern permits no statement regarding the relation of the two forms in these areas.

THE SITUATION IN NORTHERN AND CENTRAL RIO GRANDE DO SUL

The majority of specimen records from Rio Grande do Sul fall in the eastern portion of a broad band that crosses the state from east to west (fig. 4). Only five localities lie outside this zone. The samples from six localities are mixed, but the frequencies of *low* specimens vary from 37.5 to 98 per cent. Seven of the remaining sites are represented by samples containing only *low*, and 13 by samples containing only *high*, specimens.

Interlocality variability is marked within both color phases. Although this does not abolish the differences, it obscures them. A similar situation is also evident in the presumably composite sample from Pôrto Alegre in which, in contrast to all other mixed samples from a single locality, the ranges for the various parameters overlap.

TABLE 1

COMPARISON OF THE SAMPLES FROM SÃO PAULO AND PARANÁ

	Low	*High*
Frequencies		
Coloration		
Checkerboard	0	2 (+2?)
Edge-marked	3 (+2?)	0
Caudal segments		
Smooth	6	—
Indeterminate	0	1
Tubercular	0	1
Parietals		
Enlarged	5	0
Normal	0	3
Precloacal pores		
Faint	0	3
Marked	4	2
2 postgenials	4	0
2 postgenials+1 postmalar	1	5
Ranges		
Snout-vent length	88–136	197–296
Caudal annuli	15–17, 21–24 (6)	16–19 (4)
Median midbody dorsals	11.5–12 (5)	16–18 (5)
Median midbody ventrals	16–18	20–22
Caudal maximum	23–25 (4)	29 (1)

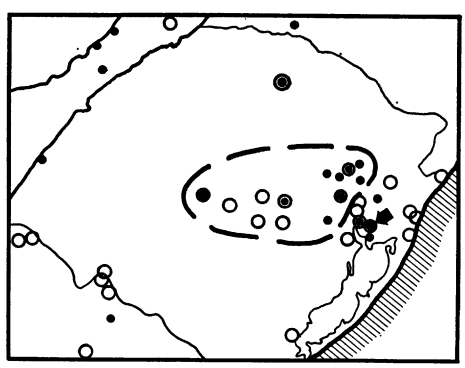


FIG. 4. *Amphisbaena*. Localities for *low* (solid circles) and *high* (open circles) specimens from Rio Grande do Sul. The arrow points to Viamão, and the heavy, dashed line surrounds the localities included in the composite sample.

TABLE 2

COMPARISON OF THE SAMPLE FROM VIAMÃO WITH THE POOLED RIO GRANDE DO SUL SAMPLE

	Viamão		Pooled Rio Grande do Sul	
	Low	*High*	*Low*	*High*
Frequencies				
Caudal segments				
Smooth	5	1	44	0
Indeterminate	0	5	2	1
Tubercular	0	9	0	9
Parietals				
Enlarged	5	0	26	0
Intermediate	1	3	31	1
Faint	0	13	2	12
Precloacal pores				
Faint	2	10	32	7
Marked	4	5	27	4
Postgenial rows number 1	2	1	9	0
Postgenial rows number 2	4	15	49	13
Ranges				
Snout-vent length	120–163 (6)	110–300 (16)	62–235 (59)	110–313 (13)
Numbers of body annuli	199–210 (6)	194–208 (16)	180–206 (59)	186–205 (13)
Mean	(203.6)	(197.8)	(190.6)	(196.3)
Numbers of caudal annuli	16–18 (5)	16–19 (15)	18–25	16–20
Mean	(17.4)	(17.5)	(21.8)	(18.5)
Autotomy site	8–9 (5)	5–7 (15)	(7) 8–9 (59)	6–8 (13)
Median numbers of midbody dorsals	12–13.5 (6)	18–20 (16)	11–14.5	16–20
Median numbers of midbody ventrals	16.5–18.5 (6)	20–24.5 (16)	14–20	21–22.5
Caudal maximum	22–24 (5)	27–34 (15)	18–26	26–32

This phenomenon is also shown when data for a group of localities from central Rio Grande do Sul are pooled and the *low* versus *high* discrimination for this composite sample is compared with that for the single sample from Viamão, collected by de Lema in a relatively restricted area (table 2). In both cases there is almost complete separation on the basis of caudal segments and parietal enlargement, although the pooled sample shows a high frequency of intermediate parietal pattern (resulting from the inclusion of the Santa Cruz sample). The Viamão sample shows better discrimination than does the pooled sample. In both, there is excellent discrimination on the basis of total and average adult size (the samples contain specimens with mature gonads and developing eggs). The ranges for numbers of body and caudal annuli overlap widely, but the relative positions of the significantly different means fall in different patterns. The Viamão sample shows non-overlapping ranges for autotomy level, median numbers of dorsal and ventral segments to a midbody annulus, and maximum number of caudal segments, whereas the pooled sample shows some overlap for two of these. The regression lines of tail on snout to vent length are not significantly different (fig. 5). There are minor differences in the relative midbody diameter; that of the *low* specimens from Viamão, but not of the pooled sample, is significantly lower than that of either *high* sample.

The marked differences in body size, plus the non-overlapping, or narrowly overlapping, ranges (of characters apparently distributed bimodally), suggests strongly that the samples being compared are drawn from specifically distinct populations.

THE SITUATION IN URUGUAY

The existence of two sympatric, but ecologically separated, forms in Uruguay was so

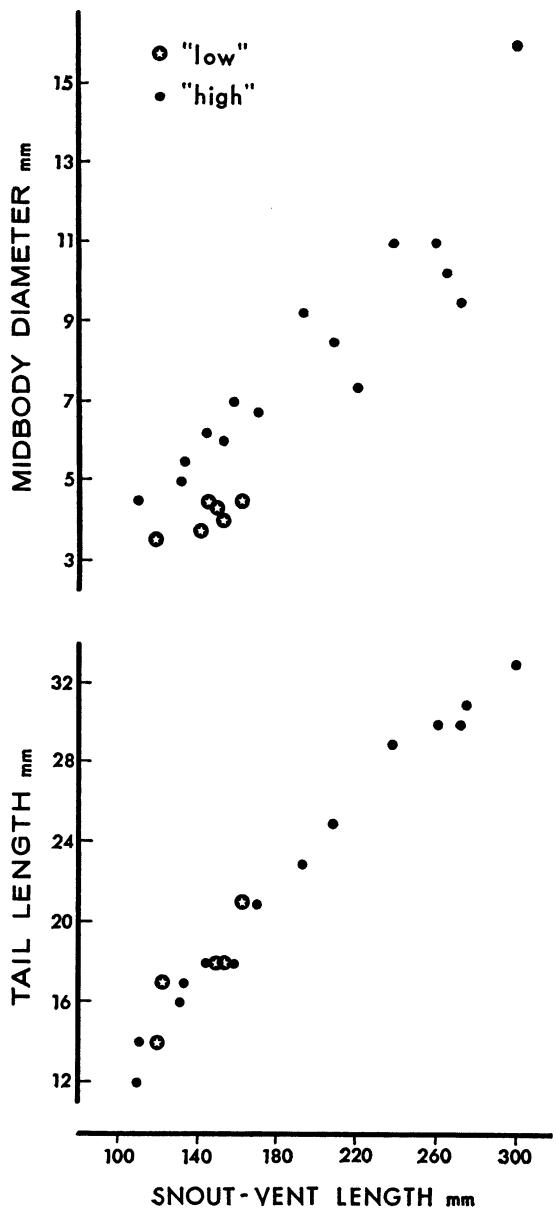


FIG. 5. *Amphisbaena*. Scatter diagram of midbody diameter and caudal length versus snout-to-vent length for the sample from Viamão, Rio Grande do Sul, Brazil.

nicely demonstrated by Klappenbach (1960) that it is necessary only to summarize his results here. His two forms correspond in general to the separation established above. Thus *Amphisbaena munoai* corresponds to the *low* sample and "*A. darwini*" to the *high* sample, respectively. The specimens of *A. munoai* differed in being smaller in total size, and in having fewer segments to a midbody annulus, constantly higher numbers of body annuli, as as well as somewhat enlarged parietal segments, and a tendency toward a single postgenial row rather than two. An examination of his material also indicates that this form shows a markedly stronger expression of the precloacal pores, which are distributed one to a segment (Klappenbach's pl. 3, fig. 7, is thus in error by omitting two sutures).

The evidence adduced and all subsequent information leave no doubt that these two forms behave as good species in Uruguay.

THE REMAINING AREAS

Various other zones yield at least presumptive evidence of two sympatric forms, but the number of records is too small and their sites are too imprecise to permit formal comparisons. Such is the situation in Misiones, Argentina, and in Paraguay.

There are no records for the province of Corrientes, Argentina, and only a few from Entre Rios. All of the latter are of *high* character pattern. The two other *low* specimens from Argentina have imprecise locality data, so that it must be assumed that the form does not occur south of Uruguay.

RESULTS

The first step in the analysis has provided evidence that the over-all sample being compared contains at least two groups of populations, respectively referred to as *low* and *high*, and that samples of these behave as good species in central São Paulo, northeastern Rio Grande do Sul, and south-central Uruguay.

RECOGNITION OF SPECIES IN SPACE

THE PRECEDING ANALYSIS immediately raises two questions: Are the categories here defined homogeneous? What are the relations of the discrete samples to one another and to populations outside the regions of overlap? The first question turns out to be of more immediate concern for the *low* than for the *high* samples. The non-dimensional approach is again useful and is here applied.

The reply to the second question is approached most easily by the presenting of a series of accounts that show the variation of each character across the range of the entire grouping. The constancy of characters, the clines they exhibit, and their correlation must serve as fundamental criteria for species discrimination. Races are recognized when they meet the criteria discussed below, under Analysis of the *Low* Specimens and Analysis of the *High* Specimens.

ANALYSIS OF THE *High* SPECIMENS

LOCALITIES OF MATERIAL: Inspection of the material suggests that the samples of *high* specimens from São Paulo, Rio Grande do Sul, and Uruguay differ in a number of characteristics, and it also indicates a number of similarities. These similarities also extend to *high* specimens from the states of Paraná and Santa Catarina (Brazil), from Bolivia, Paraguay, and Argentina.

The comparison could thus be carried out for the entire *high* sample and across its composite range.

The possibility that the *low* specimens, for instance in Rio Grande do Sul, might be conspecific with the *high* specimens from adjacent Uruguay was also tested. This hypothesis always encountered the difficulty that any *high* or *low* sample was always more similar to other samples of the same grouping rather than to samples of the opposite grouping.

It is necessary to mention the existence of a very limited series of samples of as yet uncharacterized amphisbaenids, allopatric to the specimens discussed here and "replacing them" to the south (the closest records lie in Mendoza and La Pampa, providing a hiatus of some hundreds of kilometers). These specimens differ by much higher counts of body annuli, of segments in a midbody annulus, and of caudal maximum segments, as well as by the general appearance of their cephalic segmentation. The material, which includes the holotype of *A. plumbea* Gray, will be discussed in a subsequent paper, which is being delayed in the hope that a more nearly adequate representation will be obtained. There is now scarcely any reason to suspect that the two groupings could be conspecific.

BODY ANNULI: Figure 6 shows a plot of the distribution of values of body annuli across the range. The entire assemblage has been subdivided into general zones, and the ranges of sample means (underlined values) and of individual specimen values are given for each category. Areas for which only individual specimens were available do not show the former. Solid lines separating the zones on the map indicate non-overlap, while the broken lines denote slight overlap of individual specimen values.

Two items are immediately apparent. The first is the remarkable diversity of the values along the coast of Brazil, particularly the value for the samples from northern Rio Grande do Sul. The second is the absence of any long-distance trends that would permit the plotting of isophenes for count values. Adjacent sample zones are often remarkably distinct, and trends reverse rapidly.

The highest counts ($m = 196$–203, $R = 191$–207) are found in samples from a broad zone extending across Paraguay and central Argentina and sending fingers into central Uruguay and central Rio Grande do Sul. A second and smaller high-count plateau ($m = 195$–201, $R = 191$–208) occurs in the vicinity of Pôrto Alegre, Rio Grande do Sul. Slightly lower sample means are found in extreme western Tucumán ($m = 191$–195, $R = 191$–201), in the province of Buenos Aires ($m = 193$–195.5, $R = 190$–202), in coastal São Paulo ($m = 194$–197, $R = 192$–200), in the strip of west Uruguayan localities flanking the Río Uruguay ($m = 195.2$, $R = 192$–199), on the Isla Martin Garcia ($R = 191$–194), and in northern Uruguay and coastal Rio Grande do Sul ($m = 189$–194.3, $R = 183$–199). Still

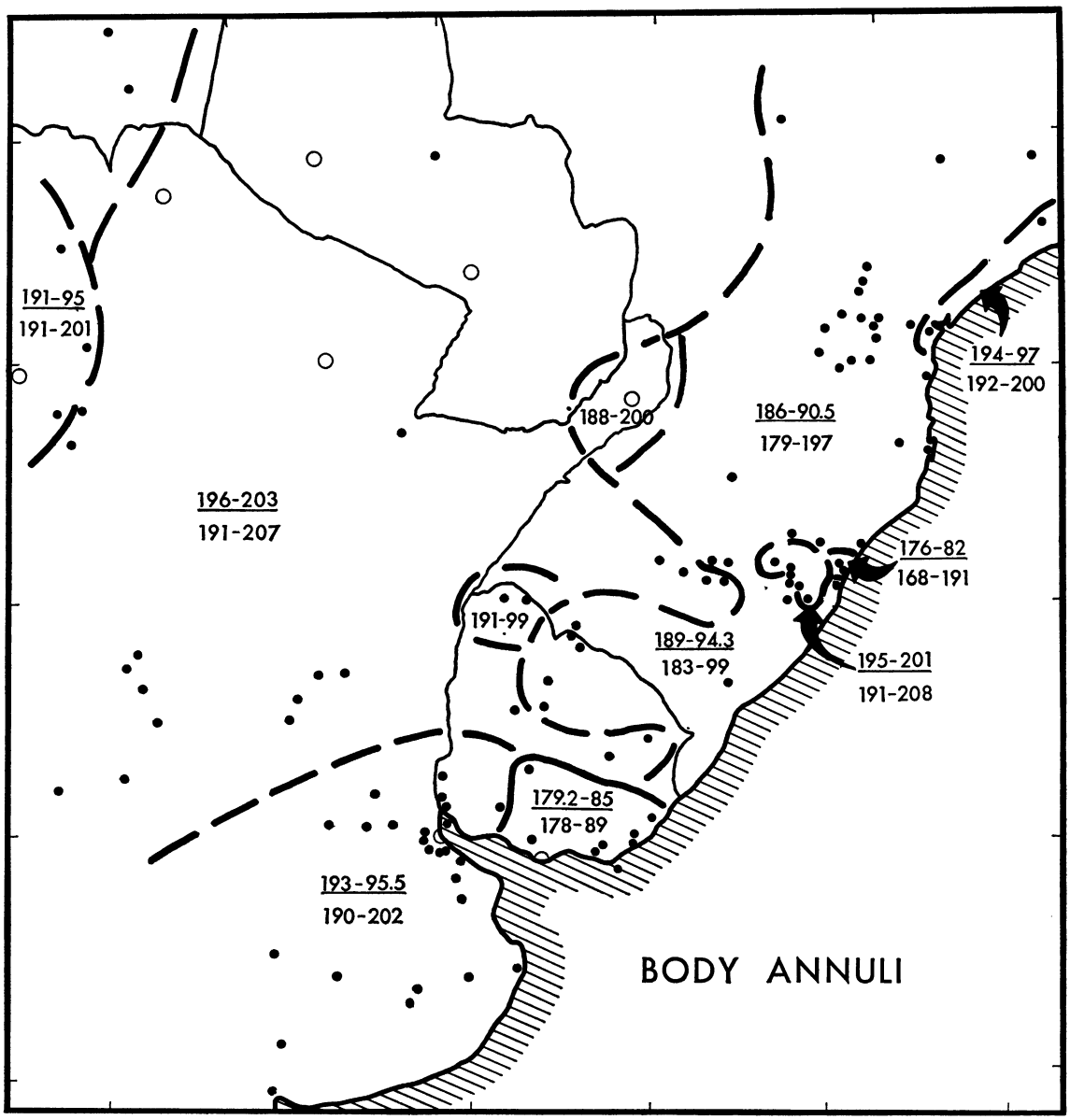


FIG. 6. *Amphisbaena darwini*. Map of the range of the *high* sample, showing the general pattern of variation of numbers of body annuli. Underlined values indicate distribution of sample means; numbers below these indicate the ranges of individual values. Solid dots show the locations from which individual specimens and samples were available; open circles show records assignable only to general regions. Their density gives a rough estimate of the reliability of the pattern.

lower values occur in inland São Paulo and in Paraná ($m = 186–190.5$, $R = 179–197$). The lowest and most significantly different values occur both in a small north coastal area of Rio Grande do Sul ($m = 176–182$, $R = 168–191$), and in the southern crescent of Uruguay ($m = 179.5–185$, $R = 178–189$). The two specimens from the Isla de Lobos off the coast fall at the lower end of this range ($R = 178–181$).

CAUDAL ANNULI: The pattern for numbers of caudal annuli is very much simpler than for numbers of body annuli (cf. fig. 7). There is

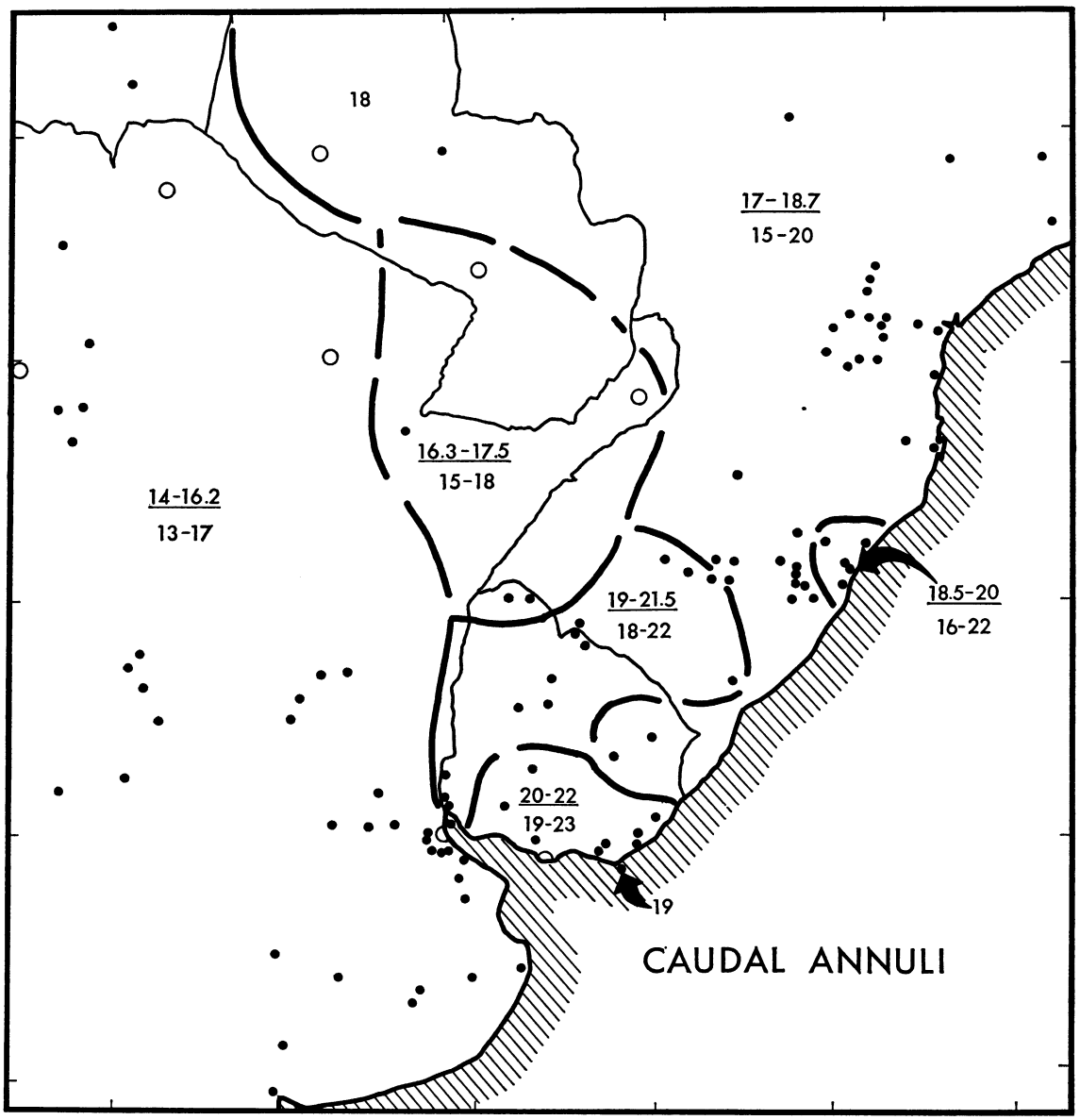


FIG. 7. *Amphisbaena darwini*. Distribution pattern for caudal annuli. Details as given in legend to figure 6.

an extensive plateau of low counts ($m=14$–16.2, $R=13$–17) that ranges southeastward from Bolivia across Argentina to the coast. An intermediate zone includes the samples from southern Paraguay, Resistencia (Chaco), and Misiones in Argentina and Artigas in Uruguay ($m=16.3$, $R=17.5$). The next higher values ($m=17$–19, $R=15$–20) come from a zone including western Paraguay, São Paulo, Paraná, Santa Catarina, and much of Rio Grande do Sul in Brazil, as well as a restricted zone in eastern Uruguay. Somewhat higher values ($m=18.5$–20, $R=16$–22) are found along the northern coast of Rio Grande do Sul inland toward Pôrto Alegre. The highest values ($m=20.5$–22, $R=19$–23) occur in a crescent-shaped zone along the southern coast of Uruguay.

The latter zone is surrounded by an area of slightly lower counts ($m = 19–21.5$, $R = 18–22$) that includes the strip along the Río Uruguay and extends northward into central Rio Grande do Sul. The specimen from the Isla de Lobos has a lower value (19) than have specimens from the adjacent coast; the values from the Isla Martin Garcia (17, 20) suggest that one specimen has its affinities on the east bank, the other on the west bank, of the river.

MIDBODY SEGMENTS: Since the general pattern for the number of midbody segments is approximately the same for dorsal and for ventral counts it has been shown only for the latter (fig. 8). The ranges for individual median values overlap widely, and even the sample means provide only limited discrimination.

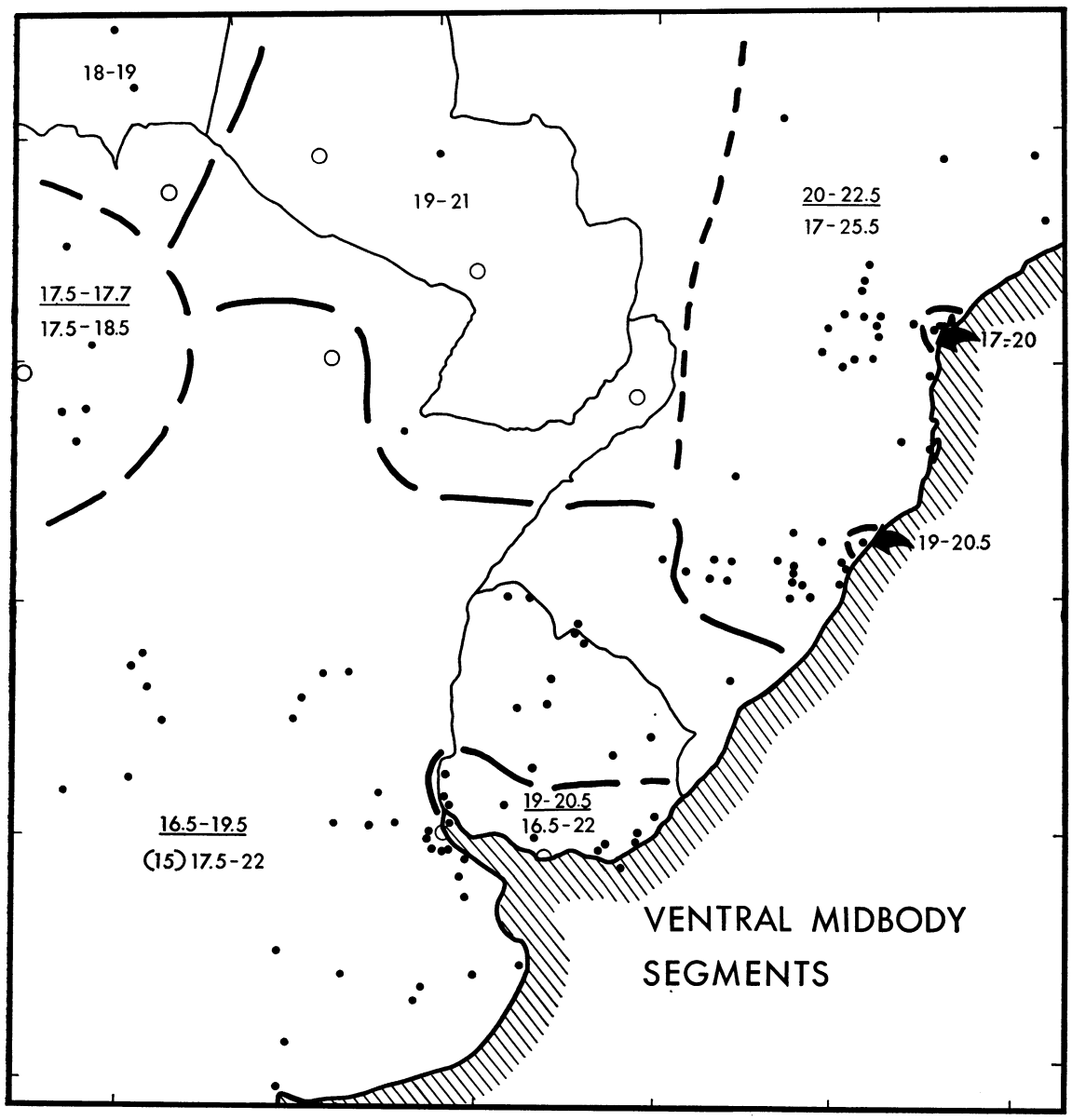


FIG. 8. *Amphisbaena darwini*. Distribution pattern for median numbers of ventral segments to a midbody annulus. Details as given in legend to figure 6.

The major separation is generally between the northern and the southern samples. Samples from São Paulo, Paraná, Santa Catarina, and northern and central Rio Grande do Sul have a range of means from 20 to 22.5 ($R=17$–22.5), and samples from Paraguay and northern Argentina are only slightly lower ($m=20.3$, $R=19.5$–20.5). An exception is formed by the coastal samples from Paranagua (Paraná) and Tôrres (Rio Grande do Sul) which have much lower values ($m=18.5-19.25$, $R=19-20.5$). The samples from the southern half of Uruguay show significantly lower values ($m=19$–20.5, $R=16.5$–22); the specimens from the Isla de Lobos fall at the upper end of this range.

The samples from most of Argentina, as well as those from southern Rio Grande do Sul and northern Uruguay, show lower values [$m=16.5$–19.6, $R=(15)17.5$–22], with the extreme western samples possibly distinct. The sample from Isla Martin Garcia is again intermediate.

MAXIMAL CAUDAL SEGMENTS: The maximum number of segments to a caudal (post-autotomy level) annulus has been plotted in figure 9. The highest values clearly occur in the northern coastal region, the zone that extends north from Santa Catarina. Slightly lower values are found in north-central Rio Grande do Sul, and still lower ones along a coastal strip extending to the southern tip of Uruguay. More inland specimens show a further reduction in counts.

CAUDAL TUBERCULATION: With few exceptions, all adult Brazilian specimens show marked tuberculation of the caudal segments (fig. 10). This condition is also observed in specimens from northern Uruguay, and in those from Misiones, Argentina. In all these the tuberculation is expressed both as a general swelling of the segment and a pronounced projection of each distal annulus. The center of each of the distal segments, furthermore, bears a distinct secondary tubercle. Samples from a few northern coastal localities in Rio Grande do Sul show only faint tuberculation (lacking the secondary tubercles), as do individuals from Pelotas in that state, from north and central Uruguay, and two specimens from Resistencia (Chaco), Argentina. All other specimens lack all aspects of caudal tuberculation, though they retain the condition of having the distal tip of the tail heart-shaped rather than cylindrical in cross section.

The correlation between this character and the one previously discussed is not so clear as might have been expected. The highest segment numbers invariably occur in specimens with a marked tuberculate pattern, but two-thirds of the count range may occur in specimens with smoothly segmented or tuberculated tails. This latter occurrence suggests that the segmental number and segmental appearance may well be independently determined. This independence of effects is also suggested by the observation that the tuberculation or segmental swelling affects all segments in a given region, including the tiny intercalated fragments that fill the interstices between the larger segments.

COLOR PATTERN: The color variability of the present population exceeds that of most other species in that the segmental pigmentation may be uniform, centrally emphasized (i.e., dotted), or asymmetrically emphasized by a variably widened marking of the anterior segmental edge. The centrally emphasized pigmentation is indicated as a rounded (rarely a squarish) dot in the center of a more or less heavily expressed general (background) pigmentation. The lateral countershading occurs both as a general fading of the background pigmentation and as a diametric or areal reduction of the ventral, heavily pigmented zone. This combination yields a dotted appearance that remains particularly noticeable along the side of the animal. On a certain number of specimens the very much lightened pigmentation and edge marking drop out by segments on the ventral surface.

The dorsal pigmentation is often so dense that it masks the presence of central pigment emphasis and edge marking in well-preserved specimens; in such specimens the dotting and edge marking become more obvious as the color fades. There may even be several concentric regions with degrees of pigment density increasing toward the segmented center.

There are two variants of the dotted pattern. In the first, the dotting extends over the dorsal surface from the nuchal region to beyond the cloaca. In the second, the dotting is highly emphasized on the anterior portion of the trunk, but fades out gradually so that the

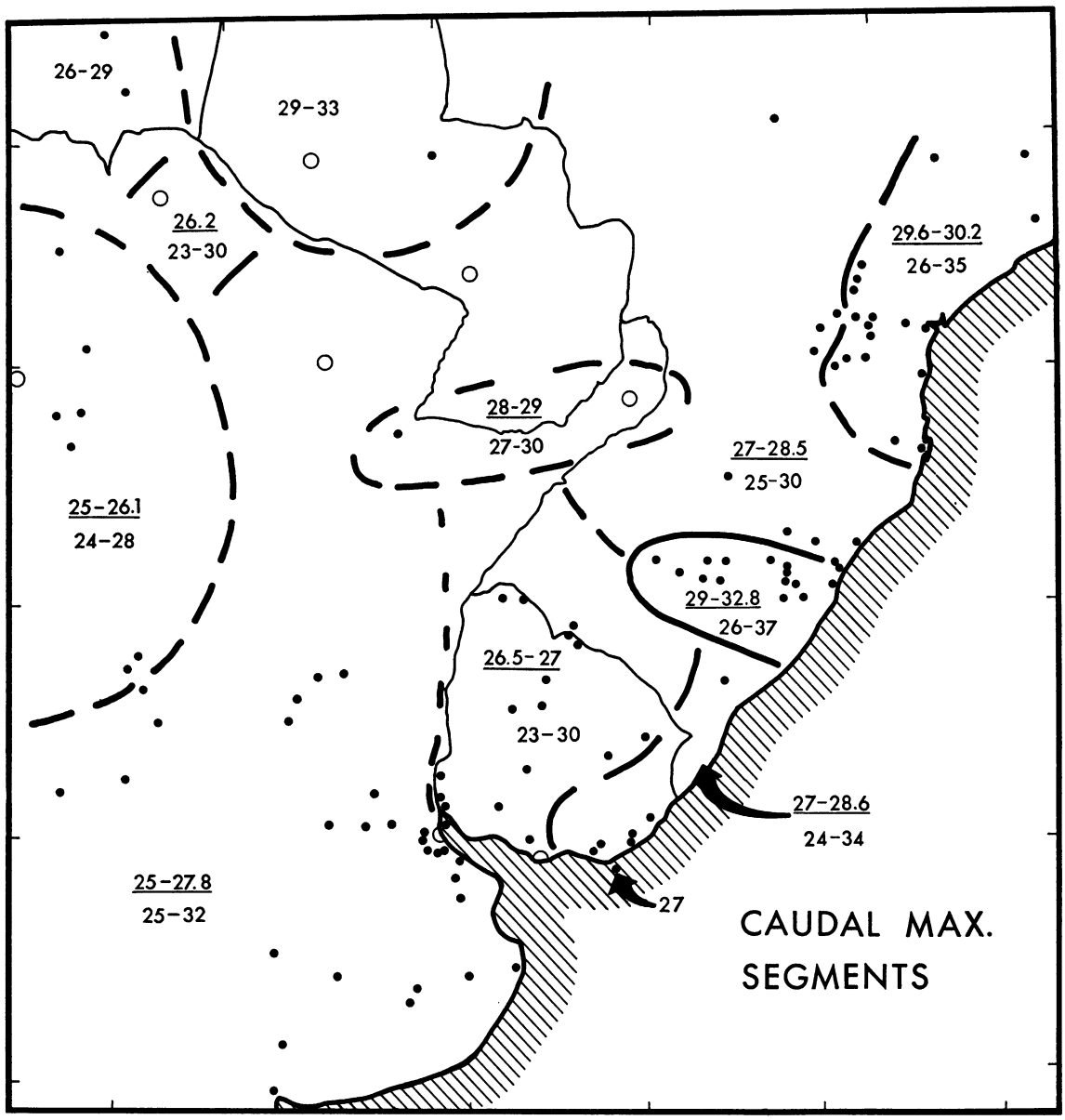


FIG. 9. *Amphisbaena darwini.* Distribution pattern for maximum number of segments to a caudal annulus positioned beyond the autotomy level. Details as given in legend to figure 6.

posterior half shows a uniform pigmentation of the segments. In both there tends to be an accentuated dotting in a halfmoon-shaped area on the sides dorsal and posterior to the cloaca. Figure 11 shows the distribution of the relative frequencies of these two variants, and indicates that the relative frequency varies from more than 75 per cent half dotted in the Tucumán region to 100 per cent entirely dotted in northern Rio Grande do Sul, Paraná, and São Paulo. The completely dotted specimens in the last region also show a high frequency of a more or less dense pigmentation of the ventral surface, suggesting that the genetic pattern determinants may here be associated with a secondary, emphasizing factor.

Another pattern, the so-called "even"

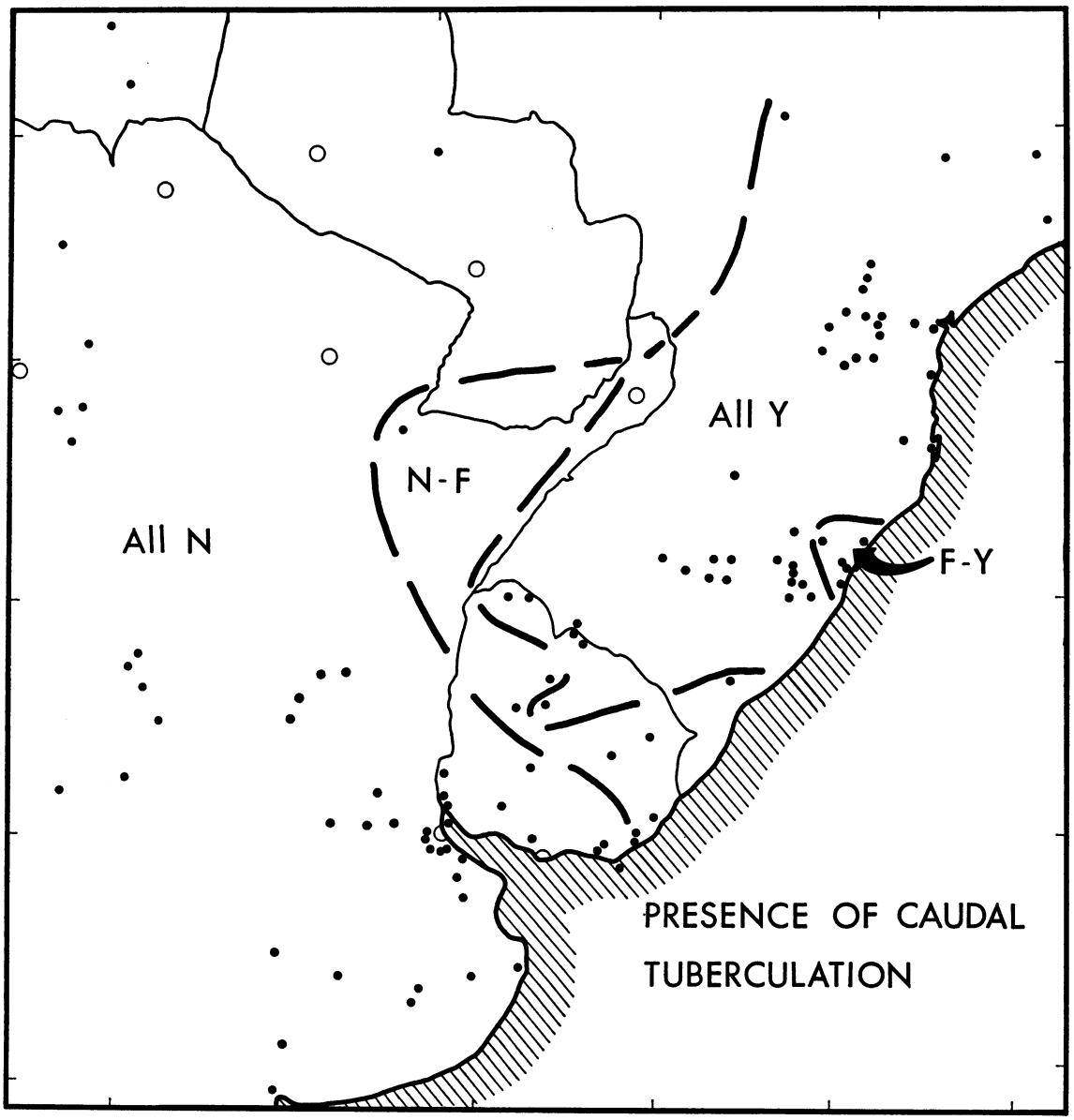


FIG. 10. *Amphisbaena darwini*. Distribution pattern for specimens having entirely (Y) or faintly (F) tuberculated caudal tips. N stands for specimens with a smooth tail, lacking all caudal tuberculation. Details as given in legend to figure 6.

coloration, occurs with a frequency of more than 80 per cent in the southern crescent of Uruguay and in varying frequencies through a more northern zone extending into south-central Rio Grande do Sul. These specimens show a complete absence of the central pigment concentration. The segments are evenly colored; in some cases they show anterior edge marking that extends laterally around the trunk and onto the sides of the ventral surface. A very few individuals show traces of the halfmoon-shaped spotted area dorsolaterally of the cloaca.

In the zones where even and dotted patterns occur sympatrically, the latter may be seen to be much less clearly expressed; they

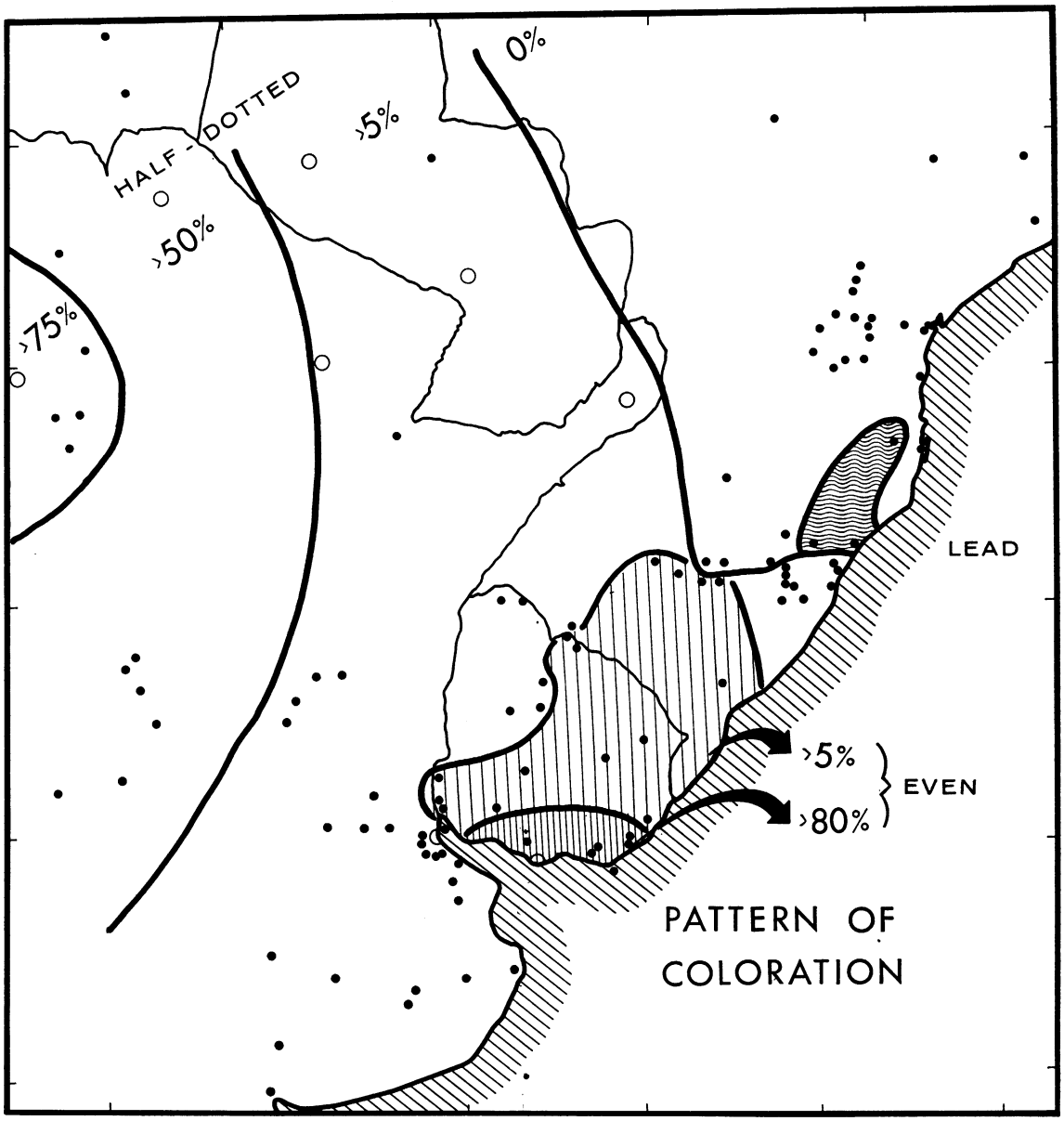


FIG. 11. *Amphisbaena darwini*. Distribution pattern of the several coloration variants. The percentage figures in the upper right indicate the zones of relative frequency of half-dotting, i.e., of specimens with the anterior portion of the body dotted and the posterior evenly covered. The vertically shaded zones indicate two frequencies of evenly colored, non-dotted specimens. The dark, wavy shading indicates the area in which lead-colored specimens occur. Details as given in legend to figure 6.

are ill defined and of irregular proportions. There are often zones from which they are totally lacking.

The specimens from the Isla de Lobos show the two variants of the dotted pattern. One specimen from the Isla Martin Garcia is faded; the other has a dotted pattern.

A group of localities (Boiteuxburgo in Paraná, specimens from Tôrres and São Francisco de Paula in Rio Grande do Sul, plus one individual from "Porto Alegre") have specimens with a "lead" coloration. The

color is lead gray, very dark and uniform in preserved specimens, although the segmental edges are emphasized by a pigment concentration, the anterior edge being most heavily marked. The segmental centers thus appear lighter than the edges. The dorsal surfaces of head and tail are very dark. Ventrally the segments appear heavily edge-marked in a continuous series. Only in the gular region and in a narrow strip along the midventral line are there light-colored segments.

TRUNK LENGTH: A number of aspects of the body proportions have been shown to exhibit geographic variation (Gans, 1959, 1964a; Gans and Rhodes, MS). Certain of these pose difficulties because there are indications in the present study that, for instance, maximum adult size may vary between the sexes (mature females are somewhat longer than males). There is no equivalent suggestion of sexual differences in hatchling size, or in regression lines, for this form. As it was impossible to check the sex of all adults by a dissection of the gonads, this size difference can only be noted.

Figure 12 shows histograms of snout-to-vent length of the several grouped samples, and figure 13 shows this characteristic projected on a map. The two illustrations confirm the fact that the northern populations are clearly the largest in terms of minimum size, (modal) size classes with maximum numbers of individuals, and maximum total size. Specimens from Uruguay and those from the vicinity of La Plata (Buenos Aires) in Argentina are of medium size; those sampled from western Uruguay are somewhat smaller. The samples from Argentina, Paraguay, and Bolivia are again composed of smaller specimens; those from the vicinity of the Federal District (Buenos Aires) are the smallest.

It must be emphasized that such comparisons of body size should most properly be based on adequate samples of specific age or condition (hatchlings, sexually mature specimens, and so on). No such samples are yet available in these non-randomly assembled collections. There is also the problem of the extremely local variant. For instance, the specimens from the Rivera-Santana area (Uruguay–Rio Grande do Sul) appear to be shorter and more slender than those from areas to the north and south, but several of them have mature gonads so that they may have been sampled from a (here poorly represented) population of smaller total size.

RELATIVE TAIL LENGTH: The several populations show marked differences in the roughly fitted regression lines for tail on snout-to-vent length (fig. 14). Such regression lines may be compared by showing the changes in the parameters a and b in the regression equation $y=a+bx$. These and the geographical changes in these parameters are shown in figure 15. The comparison of the slopes (b) suggests that the Argentine samples are most different from the Uruguayan ones; the former show certain similarities to north Brazilian specimens and these to samples from northern Rio Grande do Sul. The grouping of three localities occupied by lead-colored specimens and the north coastal grouping of Rio Grande do Sul show minor but significant differences, whereas samples from northern Uruguay, and west central Uruguay and central Rio Grande do Sul, respectively, differ from, but are closest to, the south Uruguayan samples.

The slope expresses only one of the two independent parameters defining the regression line. It seems more biologically significant (cf. Vanzolini, 1951) to compare its intercept at some standard length, thus approximating the mean tail length for a particular snout-to-vent length, preferably one for sexually mature specimens. Such a comparison has been plotted for the 250-mm. intersect (fig. 16), and the map clearly shows that the pattern is somewhat different from that for the regression coefficients.

The sample from northern Uruguay falls with the Argentine materials that have the shortest tails (24.6–27.4); the Misiones, São Paulo to Santa Catarina, and central Rio Grande do Sul lines have very similar intersects (29), and the intersect of the north coastal Rio Grande do Sul sample is somewhat higher (31.5). The samples of the south Uruguayan region are most distinct (37.6), and the Uruguayan samples peripheral to this zone differ from it (32.6–34), but remain clearly separated from the remaining areas. The lead-colored specimens, interestingly enough, have tails (36) much longer than those of specimens from surrounding areas, and almost as long as those of the south Uru-

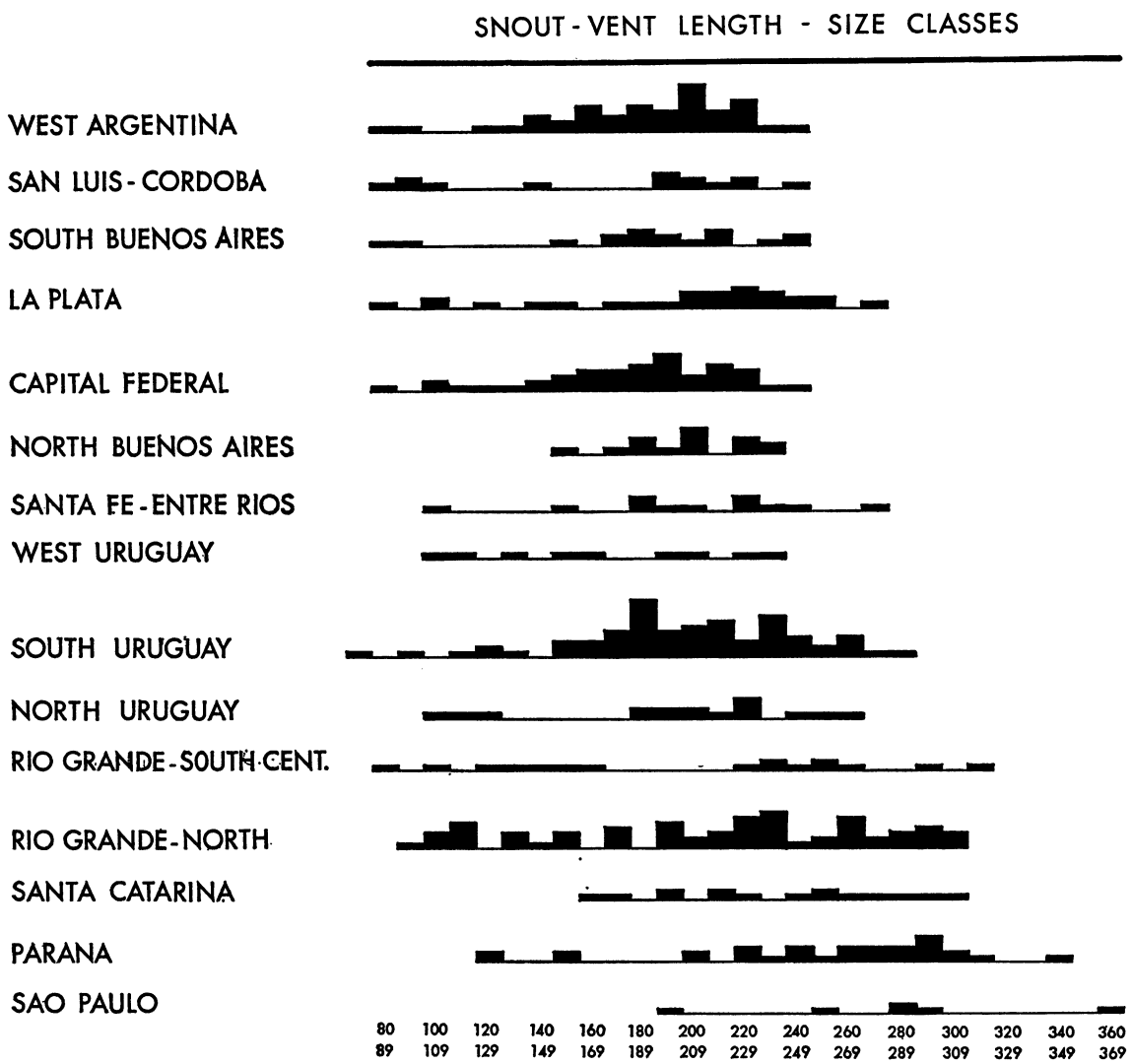


FIG. 12. *Amphisbaena darwini*. Histogram for snout-to-vent length of the several samples. Note the inadequate numbers of specimens at the terminal portion of most sample ranges. The smallest vertical unit stands for a single specimen.

guayan specimens.

SUMMARY OF VARIATION: Although the various characters appear to lack any variational concordance, they do show certain basic patterns. Emphasis on these tends to offset the superficial confusion.

1. The samples from most of Argentina exhibit remarkable constancy, with only the extreme western material showing some differences. The Argentine specimens do not differ significantly from one another in the number of caudal annuli, in the absence of caudal tubercles, or in small body size. They show only minor differences in the number of segments in a midbody annulus, the maximal number of segments in a caudal annulus, and in tail-length regression in snout-vent length. There are regular but gradual trends in the number of body annuli and in color pattern. Thus, there is little difficulty in characterizing this assemblage.

2. The specimens from the northern por-

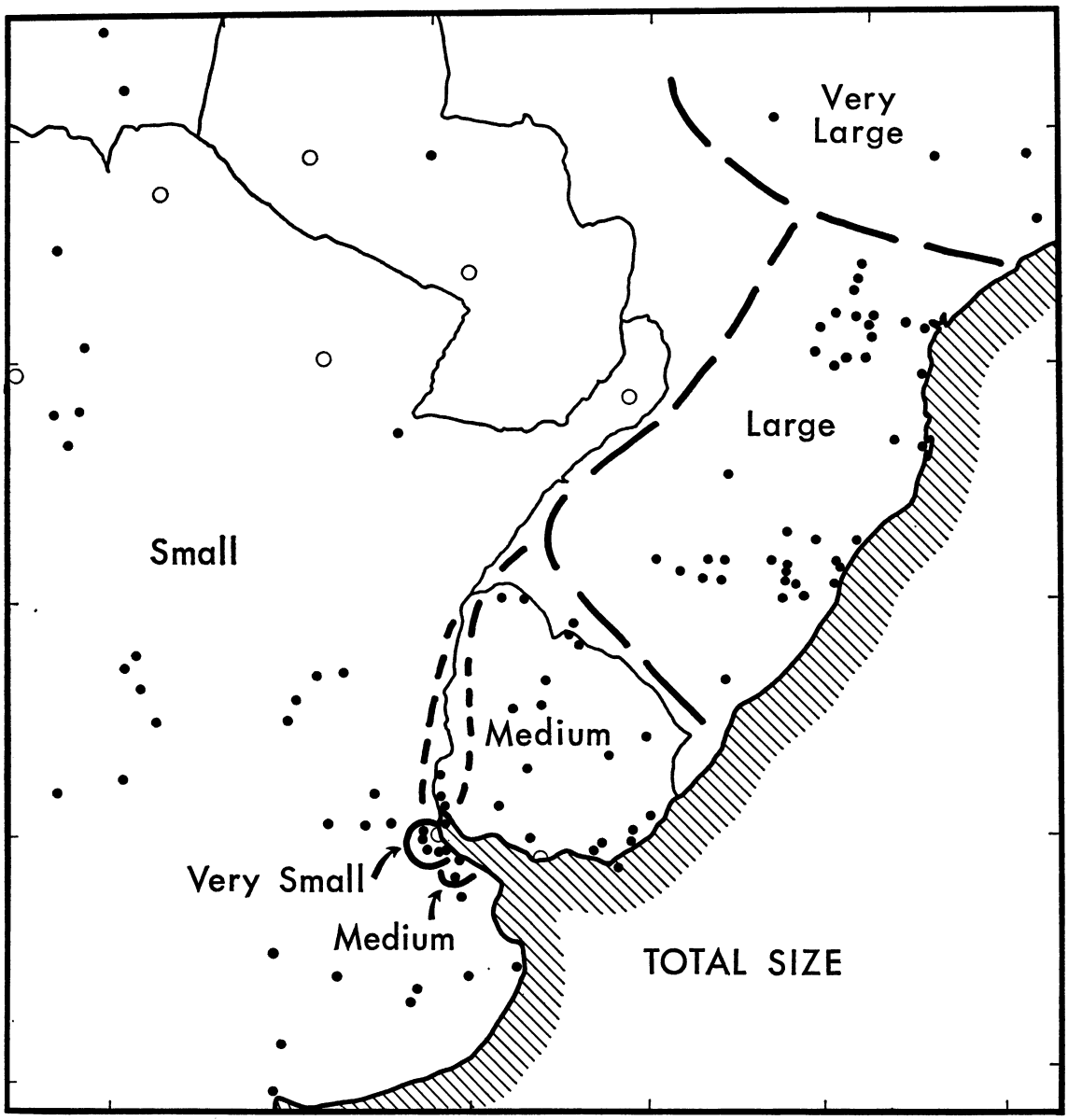


FIG. 13. *Amphisbaena darwini*. Distribution pattern for body size of adult specimens. Details as given in legend to figure 6.

tion of the range, i.e., from the states of São Paulo, Paraná, Santa Catarina, and northern Rio Grande do Sul, also form a unit. They are similar in numbers of body annuli, of caudal annuli, of segments in a midbody annulus, in marked caudal tuberculation, in distinct color pattern, and in larger total size. In relative tail length they differ from all adjacent samples except the specimens from Misiones. There is, again, little difficulty in characterizing this assemblage.

3. The specimens from the southern crescent of localities in Uruguay also form a very distinct unit. They have distinct numbers of body annuli, of caudal annuli, and of segments to a midbody annulus, and a high frequency of a distinctive color pattern. They are also characterized by a medium body size

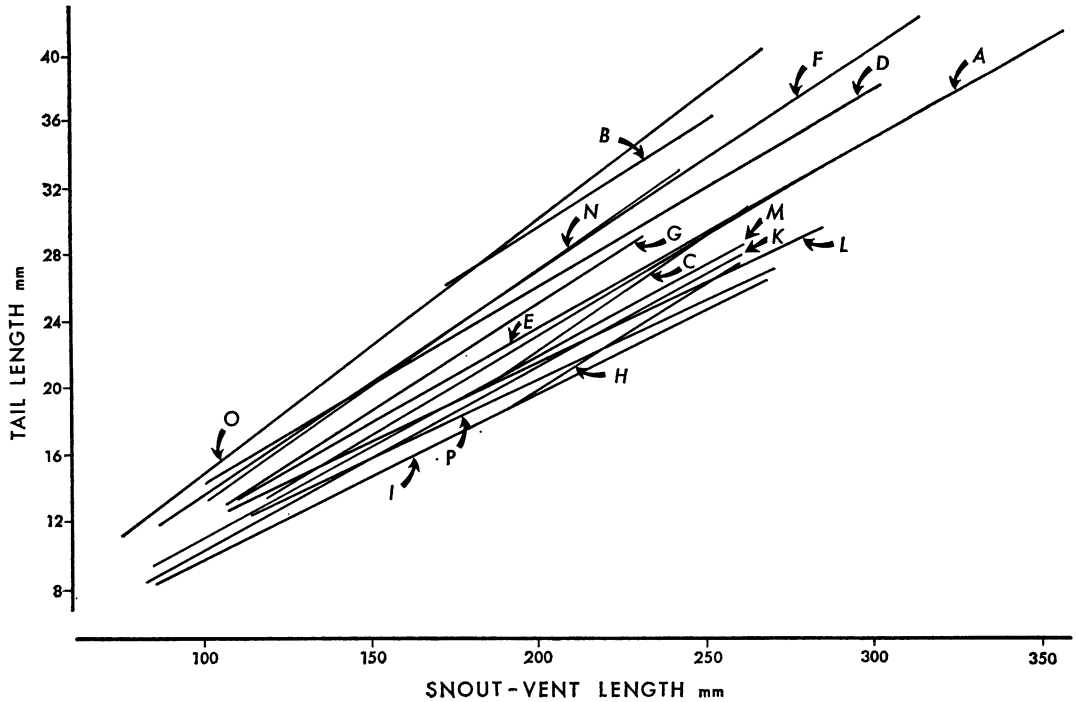


FIG. 14. *Amphisbaena darwini.* Regression lines for tail length on snout-to-vent length of the 15 samples for which these were calculated. The letters refer to the areas in figure 15.

and a relatively long, smoothly segmented tail. They can easily be identified.

4. The passage of the lower confluence of the Río Uruguay and Río de la Plata clearly coincides with the major character break in this assemblage. The limited number of samples from the east bank of the river are much closer to samples from southern Uruguay than to those from Argentina. They show a much greater similarity to the latter for body annuli, and they are intermediate in all other characteristics studied.

In contrast, the specimens from extreme northern Uruguay (Artigas) are more similar to the Argentine character pattern than to the Uruguayan. They show the caudal tuberculation pattern of the Rio Grande do Sul samples and differ from both of the others. The similarity to Argentine samples is particularly striking in view of the fact that there are scarcely any records from the adjacent states of Corrientes and Entre Rios (which include the entire west bank of the Río Uruguay). It is of considerable interest to check whether this form indeed occurs there.

The samples from central Uruguay are scanty, and each locality is represented by only one or two specimens. Further material is required for one to determine whether the irregularities seen here are significant.

5. The patterns within the state of Rio Grande do Sul are highly complex.

First, there is the São Paulo-Santa Catarina assemblage. It ranges across the northern tier of localities.

Next is a small enclave of lead-colored specimens with distinct body proportions and slight differences in other characters. The latter may turn out to be significant when more materials become available, particularly since N.M.W. Nos. 12335:6 and 12335:7, specimens without data, also combine the same characters. (M.R.C.N. No. 2066, the single specimen from Pôrto Alegre, may have been given an erroneous locality.)

Third, there are the coastal samples from Tramandaí and Osorio. These specimens differ from those from adjacent localities in the number of body annuli, in the faintness of the caudal tuberculation, and in color pattern; in these characteristics they remind one strongly of the specimens from southern

Uruguay. They appear however, to share the character pattern of specimens from more inland localities in the number of caudal annuli, the number of segments to a midbody annulus, the maximum number of segments to a caudal annulus, body size, and relative tail length.

The patterns within the rest of the state are similarly confused. Some scale characters show an approach to the Uruguayan condition, but there is a minimum of agreement between the trends of the several characters. The continuation of the caudal tuberculation across this zone forms the major common feature of these populations.

6. The values of the very small samples

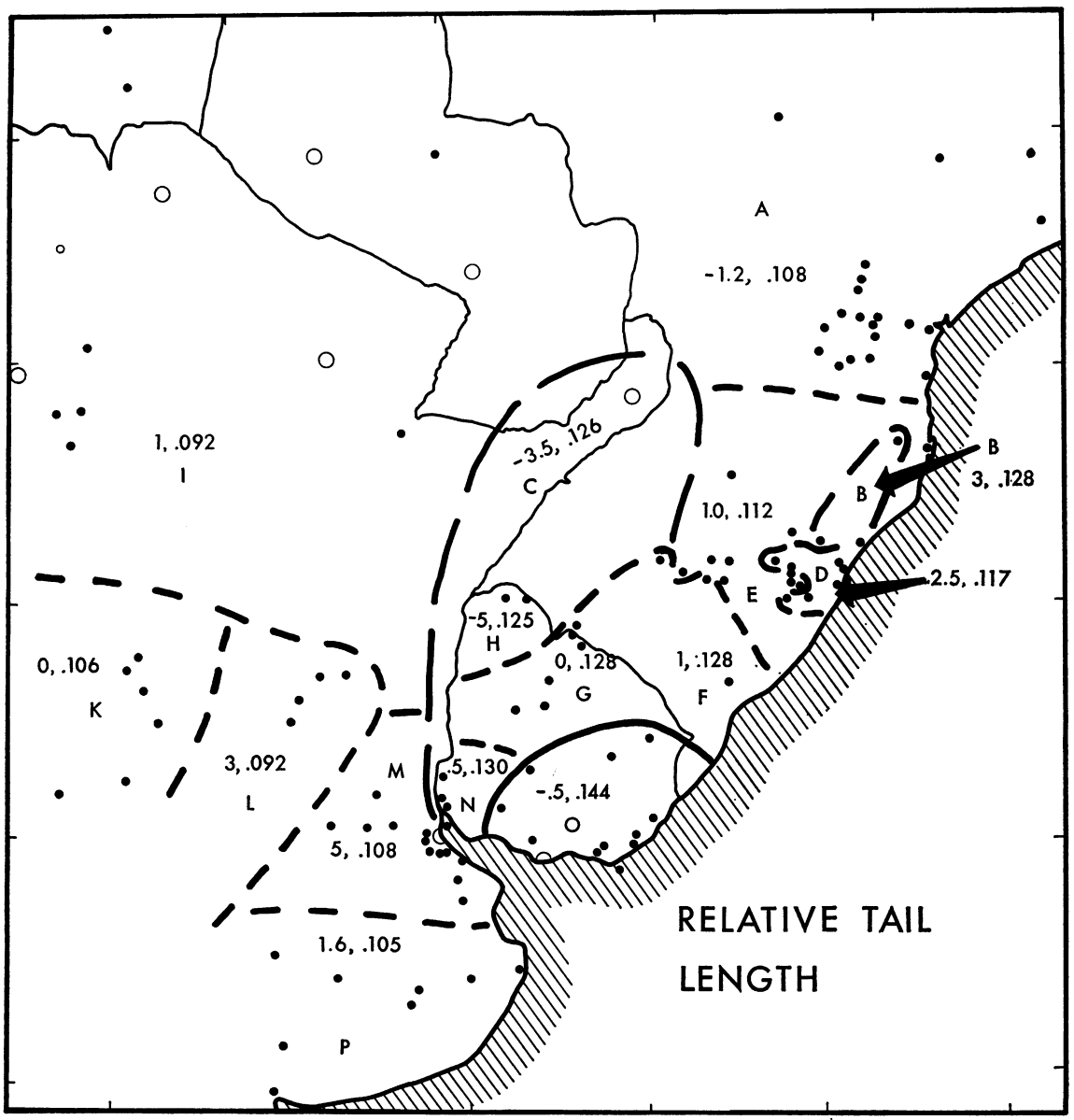


FIG. 15. *Amphisbaena darwini*. Distribution pattern for the coefficients a and b of the tail length on snout-to-vent length regression equation $y=a+bx$. The lines indicate relative differences of the slope (b). The letters refer to the actual equations in figure 14. Details as given in legend to figure 6.

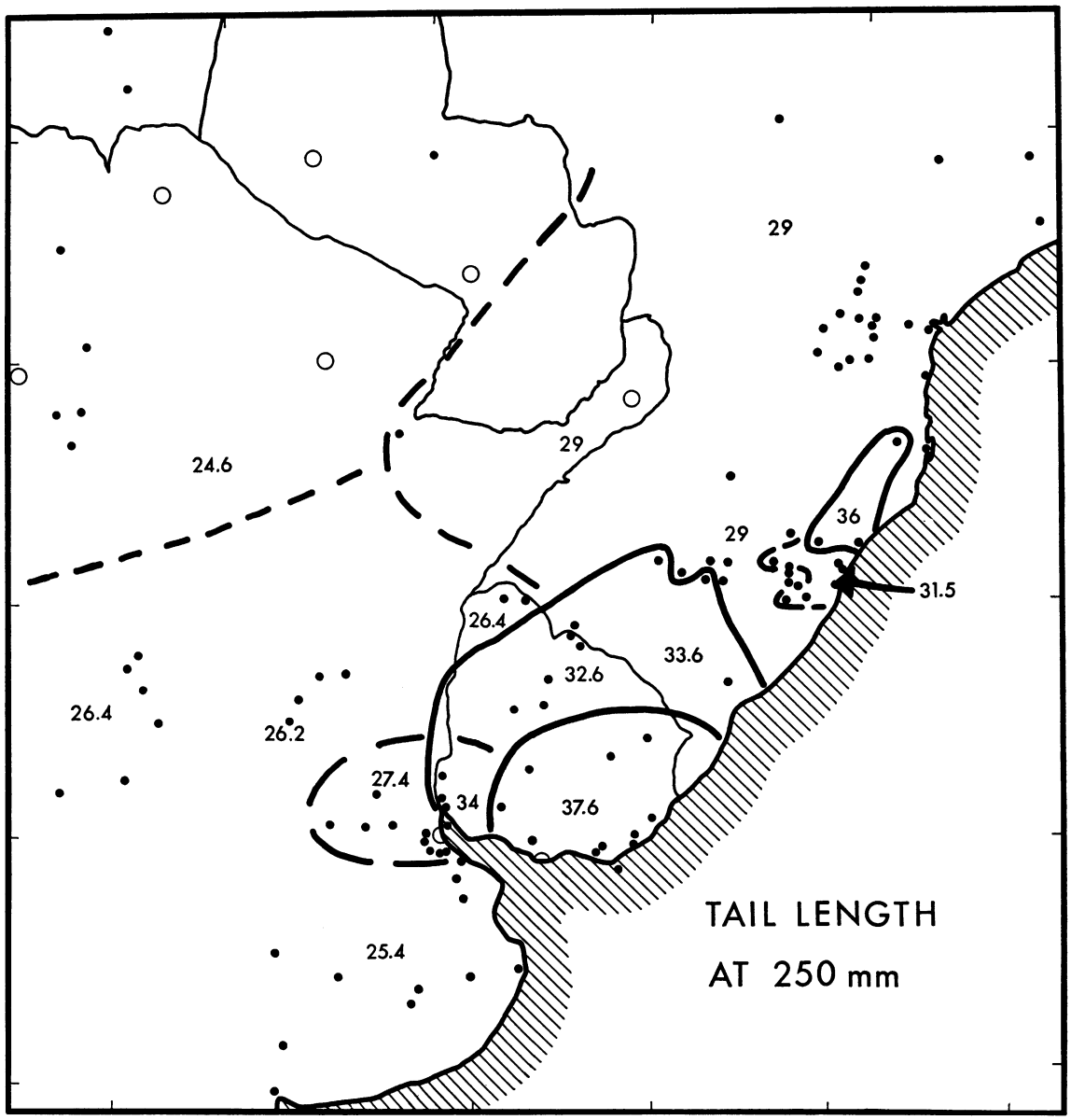


FIG. 16. *Amphisbaena darwini*. Distribution pattern for relative tail length at a standard body length of 250 mm. Compare with the pattern for the slope of the regression equation. Details as given in legend to figure 6.

from Paraguay and Bolivia agree most often with those of Argentinian samples. It is unclear whether their occasional similarity to the São Paulo-Paraná assembly implies a continuity of northern records or independent and perhaps, and fortuitously parallel, peripheral variation (cf. Mayr, 1954).

7. The character pattern of the material from the Isla de Lobos, some miles off the coast to the east of Punta del Este, Uruguay, is closest to that of samples from the adjacent mainland, but there is a distinct trend away from mainland values and for several characters those of the island specimens represent extremes.

The characteristics of the two specimens

from Isla Martin Garcia suggest that the sample either shows an *intermediate* character pattern, or the specimens each come from a different shore. An attempt to obtain additional specimens from these and other adjacent islands would be highly desirable, and such island populations might well repay intensive study.

8. In summary, the analysis has shown that there are three relatively constant sample groupings and that these are connected by more or less wide zones from which are recorded specimens and samples of intermediate appearance. The intervening zones include northeastern Argentina, parts of northern Uruguay, and much of Rio Grande do Sul, Brazil. Certain minor and geographically delimited enclaves within the latter region maintain distinct patterns.

The variability of the observed patterns may be interpreted as reflecting the effect of ecological and geographic barriers or of peripheral isolation, or a combination of these.

TAXONOMIC DECISIONS: The preceding analysis has yielded evidence suggesting that the entire *high* assemblage shows a continuous gradation in the nature or frequency of almost all characteristics. There are almost no sharp, continuous, and coincident character clines, suggesting that none of the subgroupings represents a good species. (The exception is represented by the lead-colored specimens, but the sample is too small to permit their status to be settled at this time.) The hypothesis that a single species is involved is then accepted.

This hypothesis gains further support from the observation (Gans, Huang, and Clark, MS) that specimens of this assemblage collected, respectively, at Tramandaí, Rio Grande do Sul, Brazil (C.G. No. 2770), Montevideo, Uruguay (C.G. No. 2775), and Buenos Aires, Argentina (C.G. No. 2773), shared the same chromosome counts. Kidney, lung, and heart cells grown in tissue culture uniformly show values of 12 macrochromosomes and 18 microchromosomes, giving a total number of 30.

The evidence adduced also permits decisions regarding infraspecific categories. Some dozen areas can be defined, and the component specimens can be identified by a combination of two or more characters. The question then remains if all, some, or any of these should be named. The advantages and disadvantages of the possible choices are theoretically clear, but the case is ambiguous.

The naming of all subunits reduces the decisions, but it involves a maximum possibility of error and may well be unjustified at this level of our knowledge. Furthermore, it implies some equivalence in the degree of distinctness of the several categories.

The naming of no subunits suggests that no reasonably definable major ones exist, which is clearly untrue.

The naming of the major groupings mainly furnishes a shorthand for referring to them. The names need not imply absence of intracategory variation. The major disadvantages to this procedure are that it tends to oversimplify the pattern and inevitably leaves certain regions and specimens *in limbo*. Such a result, of course, precisely reflects the biological situation and will, one hopes, encourage the next step in analysis.

Three main groupings are then characterized within this species (fig. 17). The characters to be utilized involve various aspects of the caudal morphology of the animals, as their tails appear to exhibit the most obvious variation. The first grouping (*A. darwini trachura*) consists of the specimens with a heavily tubercular tail. Its component specimens are generally large, have medium (15–20) numbers of caudal annuli, have the highest values of segments to a midbody annulus, the highest numbers of maximum caudal segments and a dotted color pattern with a marked tendency toward ventral pigmentation. This grouping includes the records from São Paulo south to Rio Grande do Sul, Brazil.

The second grouping (*A. d. darwini*) consists of specimens with a relatively long, smoothly segmented tail. These specimens are of medium size, tend toward low numbers of body annuli, have high numbers of caudal annuli, medium numbers of segments to a midbody annulus, and a high frequency of uniform coloration with lateral edge marking. This includes the specimens from south-central Uruguay and may extend into Brazil along the coast.

The last grouping (*A. d. heterozonata*) is the most distinct and consists of specimens with a very short, distally swollen tail that is cov-

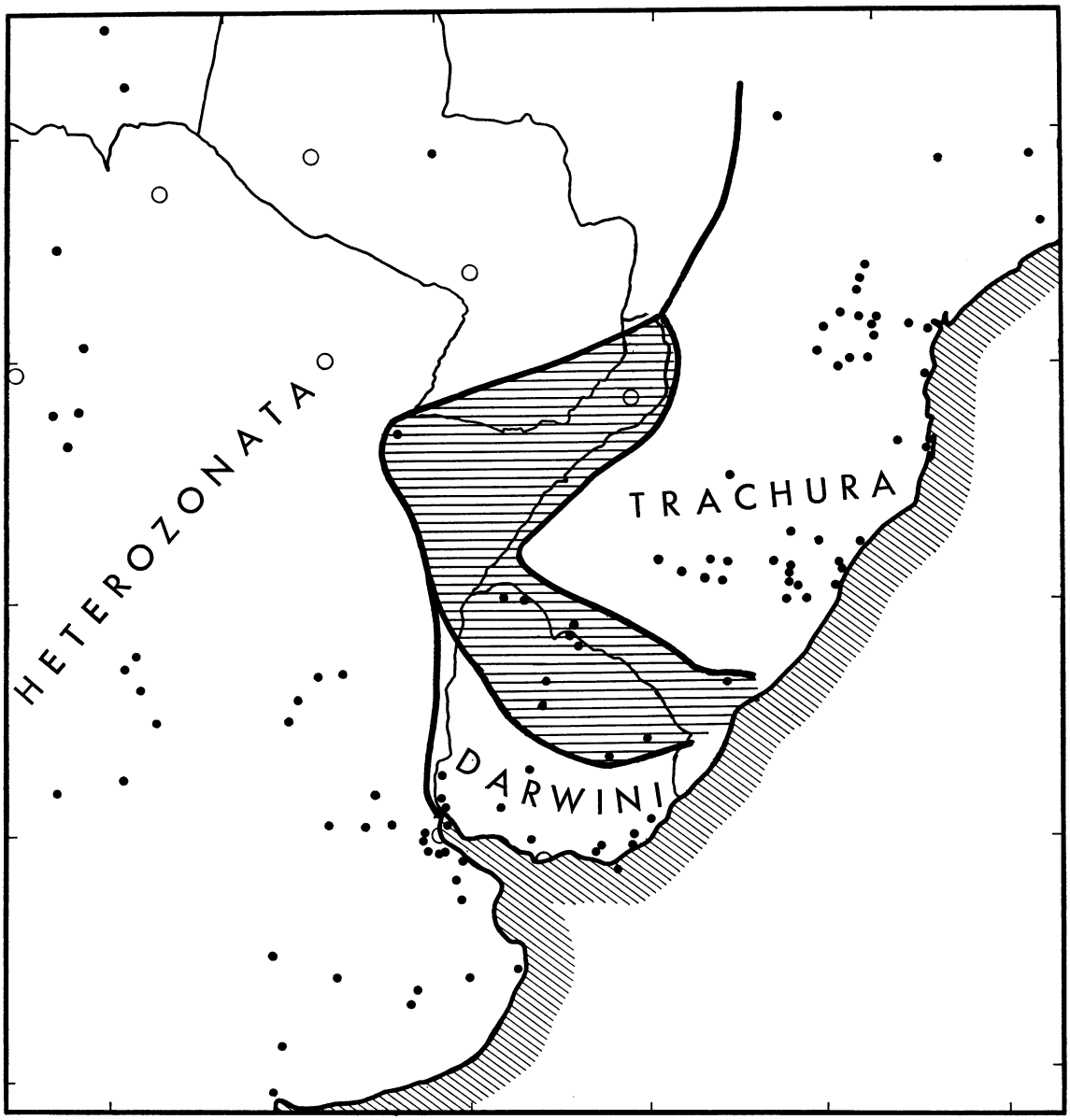


FIG. 17. *Amphisbaena darwini.* Ranges of the recognized subspecies with zones of presumed intergradation (shaded). See section Attribution of Names in text. Details as given in legend to figure 6.

ered with smooth, non-tubercular segments. These specimens are small, have low values of segments to a midbody annulus, low numbers of caudal annuli, and invariably show some incidence of half-dotted color arrangement. This grouping includes almost all records from Argentina, Bolivia, and Paraguay.

Specimens from northern Uruguay, adjacent Rio Grande do Sul, and from northeastern Argentina remain in an intermediate grouping. Refinement of this pattern then awaits the appearance of additional collections and some level of ecological correlation.

The lead-colored material is for the moment placed with the first grouping but with some reservations.

Analysis of the *Low* Specimens

Records for specimens showing the *low* pattern occur in a zone that ranges east from western Paraguay, crosses Misiones (Argentina), includes most of Uruguay, and extends northward in a belt that includes most of the coastal states of southern Brazil. The northernmost records fall in Minas Gerais, Espirito Santo, and the (new) Federal District of Brazil. The great distances between many sample localities and the small sizes of most samples indicate that there is a much more limited paradigm than was at hand for the comparison of the *high* specimens. In some regions the sample sizes are as yet inadequate for any decision regarding the status of the local forms.

The analysis of the non-dimensional species in Rio Grande do Sul indicated a unique situation. Not only were the *high* samples clearly different from the *low*, but the nature and extent of the difference varied, for instance, between the Viamão sample and the pooled sample. The *low* material from Rio Grande do Sul appeared to contain at least two forms and to offer an ideal starting point for their analysis.

Situation in Northern Rio Grande do Sul: The sample from Pôrto Alegre shows the greatest diversity, whereas samples from surrounding localities in northeastern Rio Grande do Sul appear much more uniform.

Comparison, for instance, of the samples from Morro di Coco, or Caxias, with that from Viamão shows differences in a number of characteristics, most obviously in color pattern. When the sample from Pôrto Alegre is subdivided by color patterns, it falls into two groups that similarly differ in the same characteristics.

The color pattern typical for Morro di Coco is characterized by a uniform coloration of the dorsal segments, with faint and gradual pigment emphasis that may become more marked along the sides of the trunk. There is little or no ventral lightening of the ground color, although the pigment drops out by segments near the midline of the ventral surface. Many specimens have a completely pigmented ventral surface.

In contrast, the Viamão specimens have a uniform dorsal color that fades slightly on the sides of the trunk so that the anterior edge marking becomes noticeable. The color drops out by segments some one to four segments below the lateral line, and the entire ventral surface, with the exception of the tail, is light.

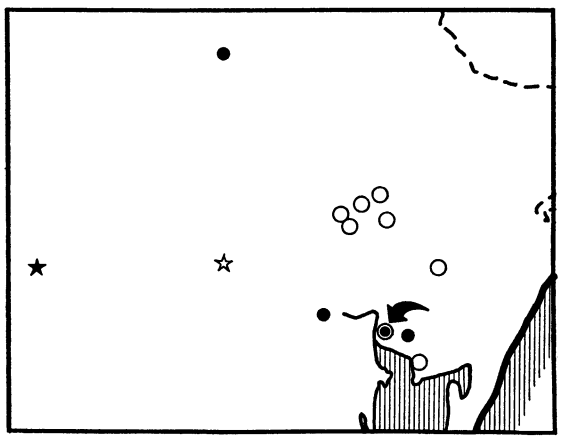


Fig. 18. *Amphisbaena*. Sketch map of the localities for *low* count specimens in the northeastern portion of Rio Grande do Sul. Open circles stand for "Coco" specimens; closed circles, for "Viamão" specimens; the arrow indicates Pôrto Alegre; the open star, Santa Cruz; and the closed star, Santa Maria.

The grouping of northeastern specimens was then divided into composite "Coco" and "Viamão" samples. The former includes the specimens from Morro di Coco, Pôrto Alegre (part), Taquara, Montenegro, Nova Petropolis, Caxias, Farroupilha, Carlos Barbosa, and Barão. The latter includes specimens from Viamão, Pôrto Alegre (part), Passo Fundo, and São Jeronimo (cf. fig. 18). Figures 19 and 20 present a comparison of various characters for these two samples. They show differences in total body size, relative midbody diameter, relative tail length, number of body and number of caudal annuli, and perhaps numbers of segments in the second postgenial and postmalar rows. The distal tip of the tail tends to be below the caudal midline in the "Viamão" specimens; it comes to a symmetrical point in the "Coco" specimens. Less marked are differences in number of segments to a midbody annulus, while other, non-meristic differences are more subtle. Thus the "Coco" sample is characterized by a slightly higher, more produced, snout, which curves down sharply near the tip. But this

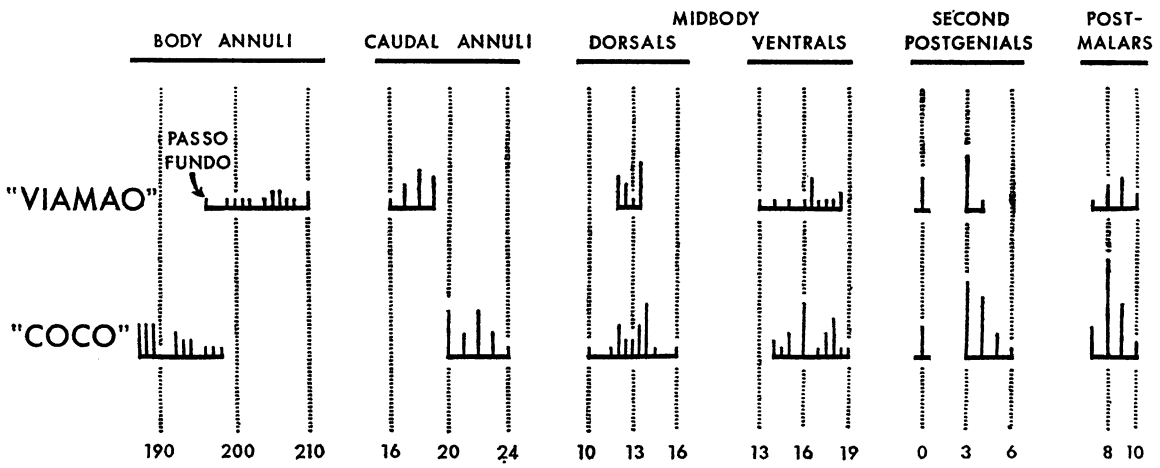


FIG. 19. *Amphisbaena*. Diagram comparing the "Viamão" and "Coco" samples for number of body annuli, number of caudal annuli, modal number of dorsal and ventral segments to a midbody annulus, and numbers of segments in the second postgenial and the postmalar row.

characteristic occurs to some degree in both forms; it is, furthermore, subject to ontogenetic variation.

The marked differences between the two samples confirm the fact that they have been selected from distinct populations. There is no evidence for strict sympatry; the critical sample from Pôrto Alegre is combined from specimens deriving from some half dozen museums. Even if the labels represent more than the shipping points or the residence (or residences) of the donor (or donors) the term "Pôrto Alegre" might refer to any part of an area some 20 kilometers across. The collection includes no material from another locality in which the two forms both occur. A decision regarding their relationship must then be based on the characteristics and distribution of samples across the entire range.

In order to facilitate comparisons, the several characters have again been plotted on distribution maps (figs. 21–28). These show the variation of the characteristics sufficiently well to permit the proceeding directly into a discussion of a comparison of the samples.

COMPARISONS TO SOUTH: Three distinct sample groupings of *low* specimens occur in the zone south of the discrimination region, namely, those from Santa Cruz, from Santa Maria, and the large but very homogeneous assemblage (Klappenbach, 1960) from Uruguay.

The sample from Santa Maria is very close to the "Viamão" grouping. The number of caudal annuli for the one specimen with an entire tail is slightly high, as is its relative tail length. There are no significant differences in head shape, color pattern, total size, body diameter, number of body annuli, and gular arrangement. Other characters are also in good agreement.

The sample from Santa Cruz (the label gave no state and the locality could have been misassigned) contains 39 specimens; it thus is the largest from a single locality. Unfortunately the specimens are somewhat faded, and the coloration poses other problems. It agrees with that of the "Coco" sample in its even dorsal color and slight central pigment emphasis, but also gives the impression of some edge marking; the degree of pigmentation and the size of the pigmented area decrease in parallel along the sides to produce the countershading. The nasal region shows a marked curvature. In body size these specimens appear equal to or larger than those of the "Coco" sample, with which they also agree in relative tail length, midbody diameter, number of caudal annuli, gular segment number, and in the rounded nature of the distal tip of the tail. The numbers of body annuli show a greater range which overlaps part of that of the "Viamão" sample; the modal region for this character is in excellent agreement with that of the "Coco" material. The number of

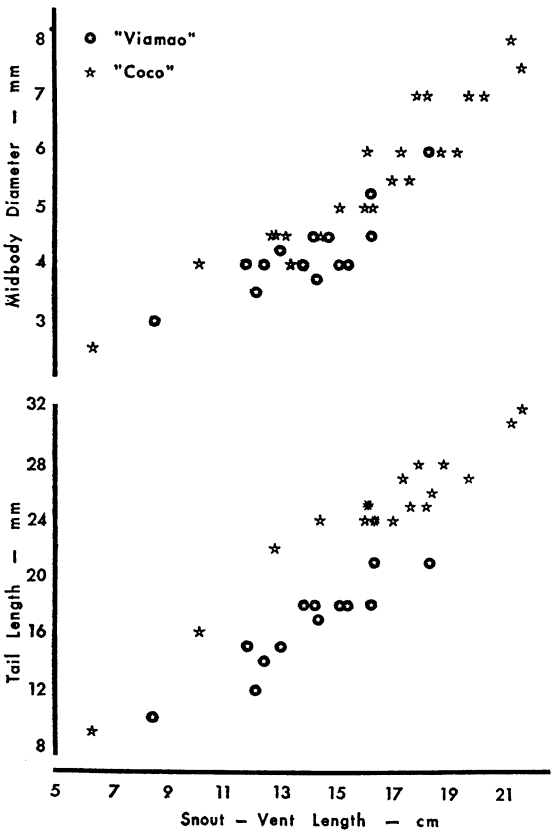


FIG. 20. *Amphisbaena*. Scatter diagrams comparing relative midbody diameter and tail length to snout-to-vent length for specimens of the "Viamão" and "Coco" samples.

segments varies. That to the dorsal half of a midbody annulus is equivalent to that of the "Coco" samples; that to a ventral half is greater than that of the latter and very much greater than that of the "Viamão" sample. The sample seems much closer to the "Coco" than to the "Viamão" sample; the differences from the former are relatively minor.

The Uruguayan material available for comparison is restricted to a series of samples from United States and European museums and to a sizable series donated by Dr. Klappenbach. Data from the original description were also considered, but the multiple paratypes of *A. munoai* were not borrowed under the mistaken impression that the form was endemic to Uruguay.

The rostral zone of these specimens is markedly curved. The bend achieves greatest curvature in the middle of the interprefrontal suture. The dorsal segments are evenly pigmented. Laterally they show some mottling, which in some zones leads to a central pigment emphasis or even a dotting, but in other regions there is a more or less emphasized marking of the anterior edge. The color fades and drops out a few segments below the lateral sulci. The ventral surface of the body is clear; that of the tail may be partly pigmented. The nasal region shows very marked curvature. The body size of the very large sample suggests that the form is somewhat smaller than the "Viamão" sample, and very much smaller than the "Coco" sample. In relative tail length it is not significantly different from that of "Viamão"; sample midbody diameter is smaller than that of "Viamão," very much smaller than that of "Coco." The mean number of body annuli is different from that of the "Viamão" sample, although the ranges overlap. The number of caudal annuli is intermediate, but much closer to "Viamão." The gular arrangement, shape of the caudal tip, and numbers of segments to the dorsal half of the midbody annulus are close to the pattern found in "Viamão"; the number of ventral segments is intermediate yet closest to "Viamão." Other characters do not differ significantly. The general pattern is one of resemblance to the "Viamão" sample, though certain characters show significant differences. These differences from "Viamão" generally make the Uruguayan material more distinct from the "Coco" sample. The Uruguayan sample does not appear to be intermediate between "Coco" and "Viamão."

COMPARISONS TO WEST: Four separate comparisons are needed for the western region. They are, respectively, with the specimen from Itaqui (Rio Grande do Sul), the samples from Misiones (Argentina), the series of specimens from Paraguayan localities, and the single specimen labeled "Nord-Chaco."

The single Itaqui specimen (not at hand when this report was written) unfortunately had an autotomized tail. It shows the "Coco" color pattern. Its body size appears to place it closest to the "Coco" range, as does the number of dorsal segments to a midbody annulus. The midbody diameter is closer to that of the "Viamão" sample. The number of

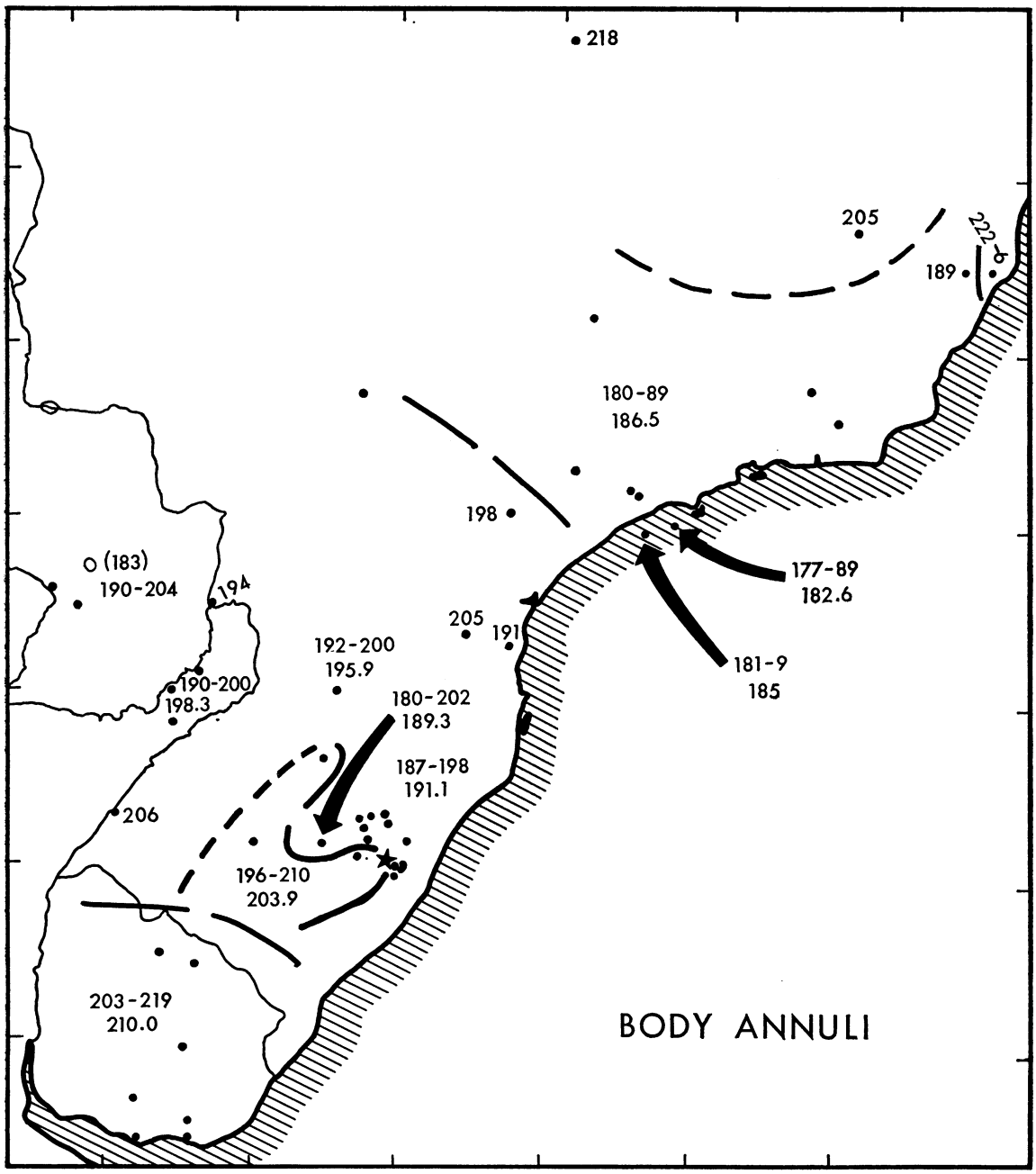


FIG. 21. *Amphisbaena*. Map of the range of the *low* sample, showing the general pattern of variation of numbers of body annuli. Sample means are shown to the nearest tenths. The "Coco" and "Viamão" (including the specimens from Santa Maria) samples are shown as single values. The solid dots show the location from which individual specimens and samples were available; the open circles show records assignable only to general regions. Their scatter gives a rough estimate of the reliability of the pattern in a particular region. The star indicates the location of the sample from Pôrto Alegre.

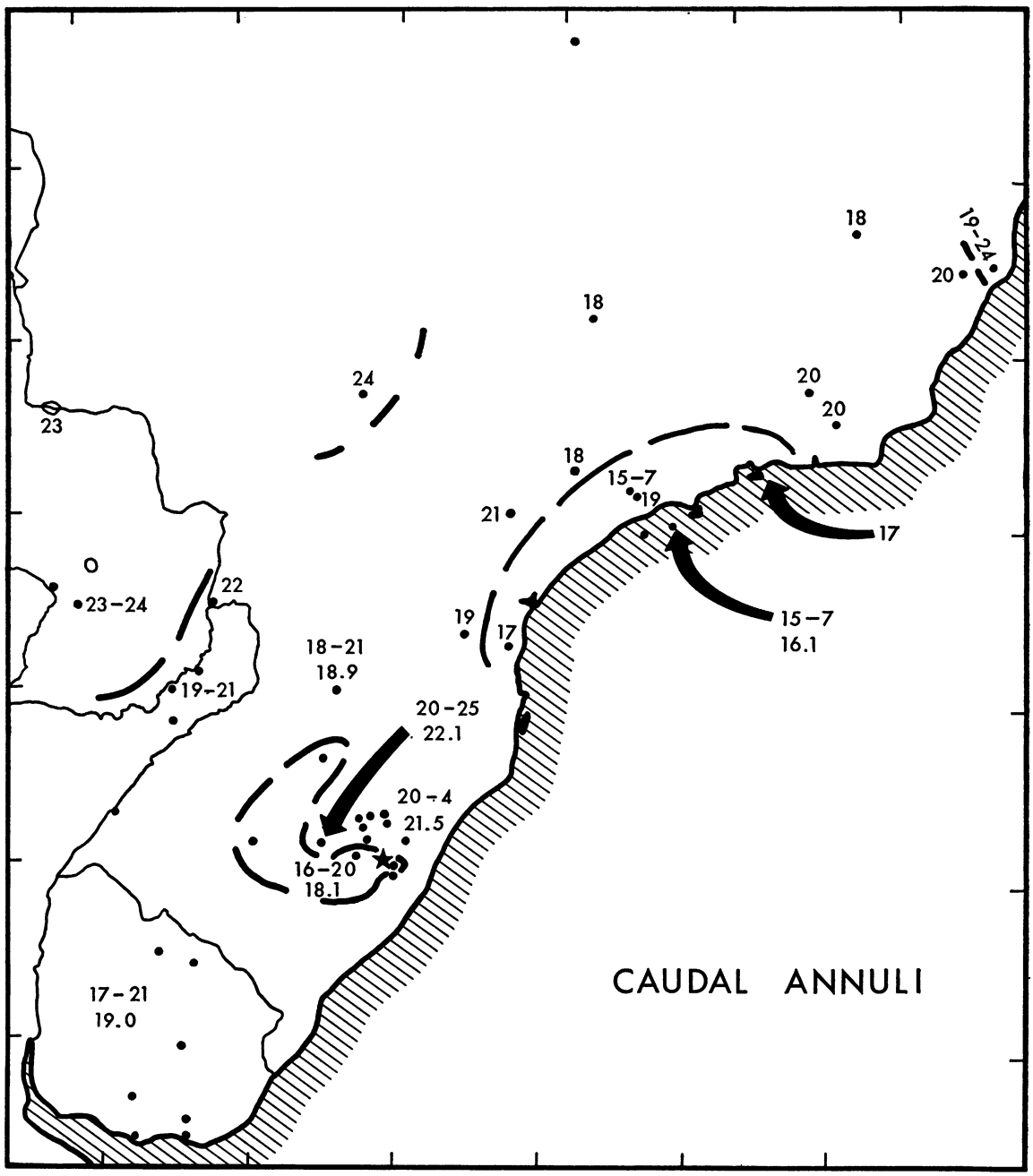


FIG. 22. *Amphisbaena.* Distribution patterns for caudal annuli. Details as given in legend to figure 21.

body annuli is high—closest to that of the "Viamão" sample and well within the range of the Uruguayan material. Other characters do not permit additional discrimination, except that the caudal autotomy level is lower than that of any specimen from the southeastern region; it falls within the range of Misiones specimens.

The sample from Misiones shows some internal variation. All its specimens, except the one from Oro Verde, have a produced, curved, rostral tip. The one from Oro Verde

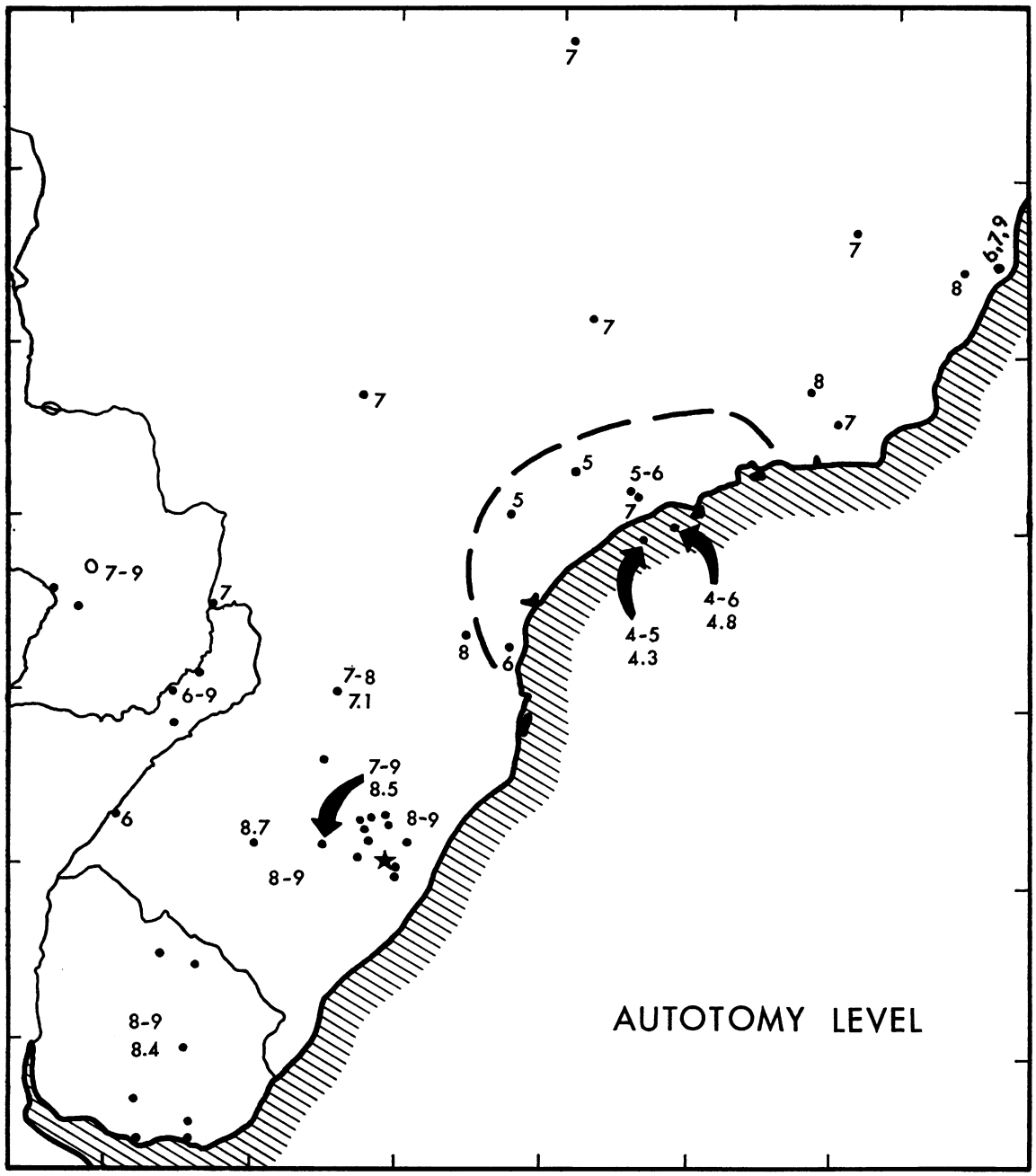


FIG. 23. *Amphisbaena*. Distribution pattern for numbers of the caudal annulus bearing the autotomy site. Details as given in legend to figure 21.

has a relatively flattened head, with only traces of the rostral curvature. The coloration of most specimens resembles the "Coco" pattern; all but an irregular midventral zone is dark, and the dark segments there drop out in a checkerboard fashion. The Oro Verde specimen shows some tendency toward a light central dot on many dorsal segments. It is also the only one with a single row of postgenials, and no postmalars, a condition that is com-

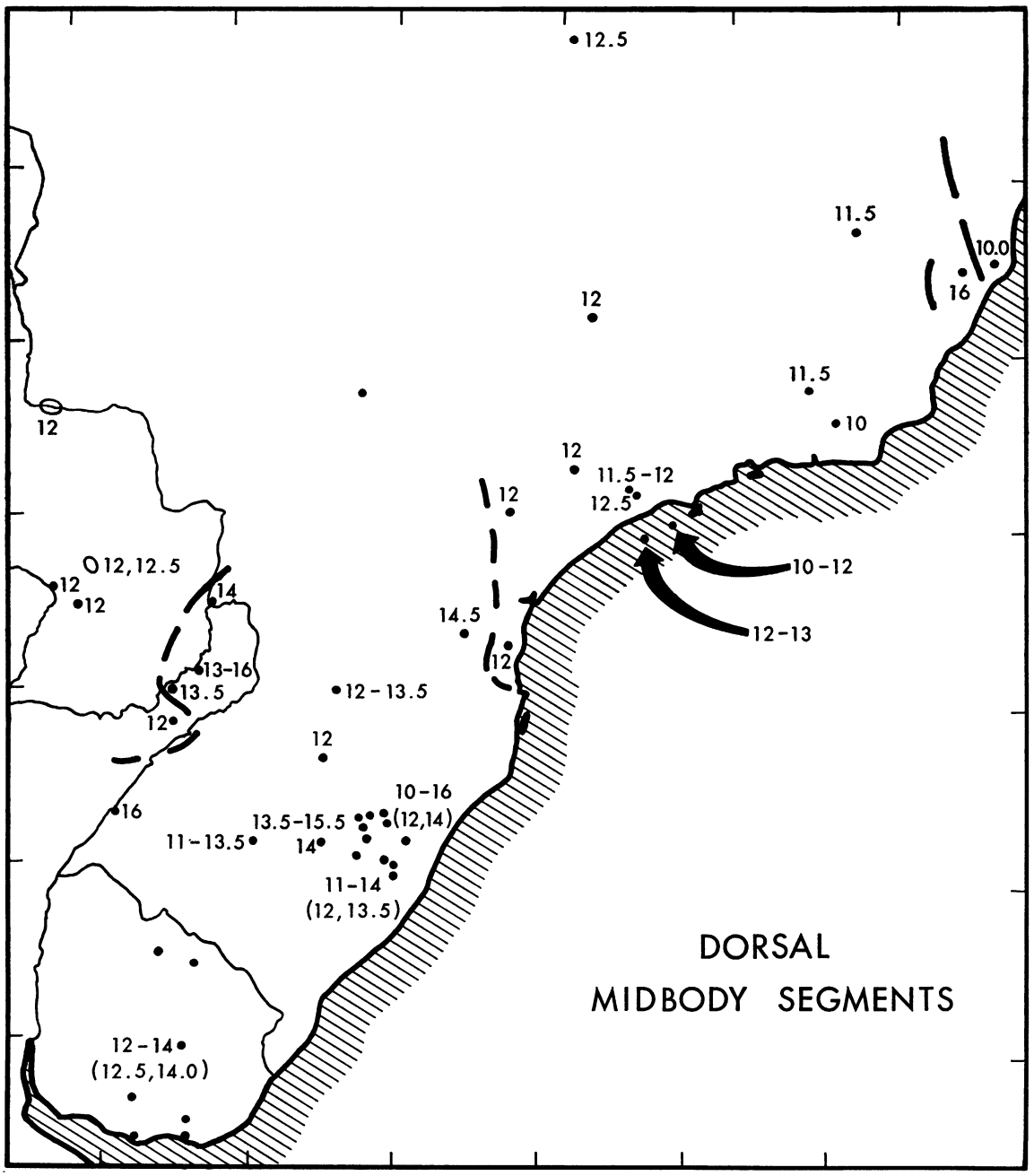


FIG. 24. *Amphisbaena*. Distribution pattern for median numbers of dorsal segments to a midbody annulus. Underlined figures in parentheses give modal values. Details as given in legend to figure 21.

bined with the participation of the first three body annuli in the temporoparietal zone of enlarged segments. The remaining specimens show the same pattern as the southeastern material, in which segmental enlargement involves the first two body annuli and a dorsal intercalated half-annulus. The body size of the Misiones sample is intermediate, and the relative tail length falls just on the lower edge of the range of that of the "Coco" sample.

Midbody diameter and number of dorsal segments agree with the values for the "Coco" sample. The number of body annuli tends to be lower than that of the "Coco" sample, as is the number of caudal annuli. The caudal tip is symmetrical. The site of the autotomy level ranges closer to the cloaca than in any but the Itaqui specimen, the value of which agrees with that from Oro Verde. The sample from Misiones, and possibly that from Itaqui as well, apparently belong to the "Coco" assemblage.

The Paraguayan specimens come from a limited scattering of sites; almost half of them lack further data. The head and rostral region appear flattened, without the swelling and curvature previously mentioned. The coloration resembles a variant of the "Coco" pattern. It is more or less even (as far as may still be determined from the faded specimens) and drops out by segments to provide a light midventral zone of variable size. The cloacal zone often remains light, even though the more anterior ventral surface is entirely covered with pigmented segments.

All specimens lack postmalars, and their three anteriormost body annuli participate in the temporoparietal region of enlarged segments, which gives them the appearance of a longer head. Only the Río Apa specimens (and one marked "No Data") have one postgenial row instead of two. The Paraguayan specimens are even smaller than the Uruguayan ones. Their relative tail length is that of the "Coco" sample, whereas their thinner body diameter approaches that of specimens from the "Viamão" sample. The body annuli range widely, higher than the values of the "Coco" sample; the number of caudal annuli is significantly the highest, falling in the upper end of the range of the "Coco" sample. The site of the autotomy annulus again agrees with that of Rio Grande do Sul specimens. The number of dorsal segments to a midbody annulus is low, and the caudal tip is asymmetrical. The characteristics of the assemblage are quite marked, and it represents an easily definable grouping. Certain of these differences do, however, appear somewhat randomly in the Misiones sample, particularly in the specimen from Oro Verde.

The single specimen from the northern Argentinian Chaco (Z.S.M. No. VI) differs markedly from the material previously discussed. It has a much more bluntly terminating snout, without the produced curving of the rostral tip or the cephalic flattening of the Paraguayan specimens. The coloration consists of an even emphasis of the dorsal segmental surfaces, which are separated by light intersegmental and annular sutures. Laterally, the pigmented area is reduced to an edge marking that drops out at some variable level on the ventral surface. The number of caudal annuli (17) and the count of the autotomy level (seven) fall lower than do those of any other specimen from the western portion of the range. Instead of being the same diameter, the tail is somewhat narrower than the posterior trunk and comes to a symmetrical tip. The relative tail length (148+15) and midbody diameter (4) fall lower than those of any other specimen. This individual apparently does not belong to any of the forms here recognized.

COMPARISONS IN NORTH-CENTRAL RANGE: The zone that includes the states of Santa Catarina and Paraná contains one adequate sample from Nova Teutonia, and individual records from Joinville (Santa Catarina), Rio Negro, Piraí, and Foz de Iguaçu (Paraná).

The specimens from Nova Teutonia and the individual from the other inland locality of Foz de Iguaçu share the "Coco" color pattern. There is relatively little ventral lightening, although some ventral segments show a bleeding of pigment. The snout is rounded and shows some curving and producing of the rostral zone. The parietals are relatively small, and there is an extra intercalated half-annulus in the nuchal region. Adult size and body diameter resemble those of the "Coco" sample, although the relative tail length is lower, falling in the "Viamão" range. Both the number of body annuli and the number of caudal annuli depart somewhat from the range shown by the "Coco" sample, in each case toward the "Viamão" condition. The number of caudal annuli shows a slight reduction. Numbers of segments to a midbody annulus are not significantly different from those shown by the "Coco" sample, and the caudal tip is rounded. Although a few of the characters show trends in the direction of the "Viamão" sample, many characters show

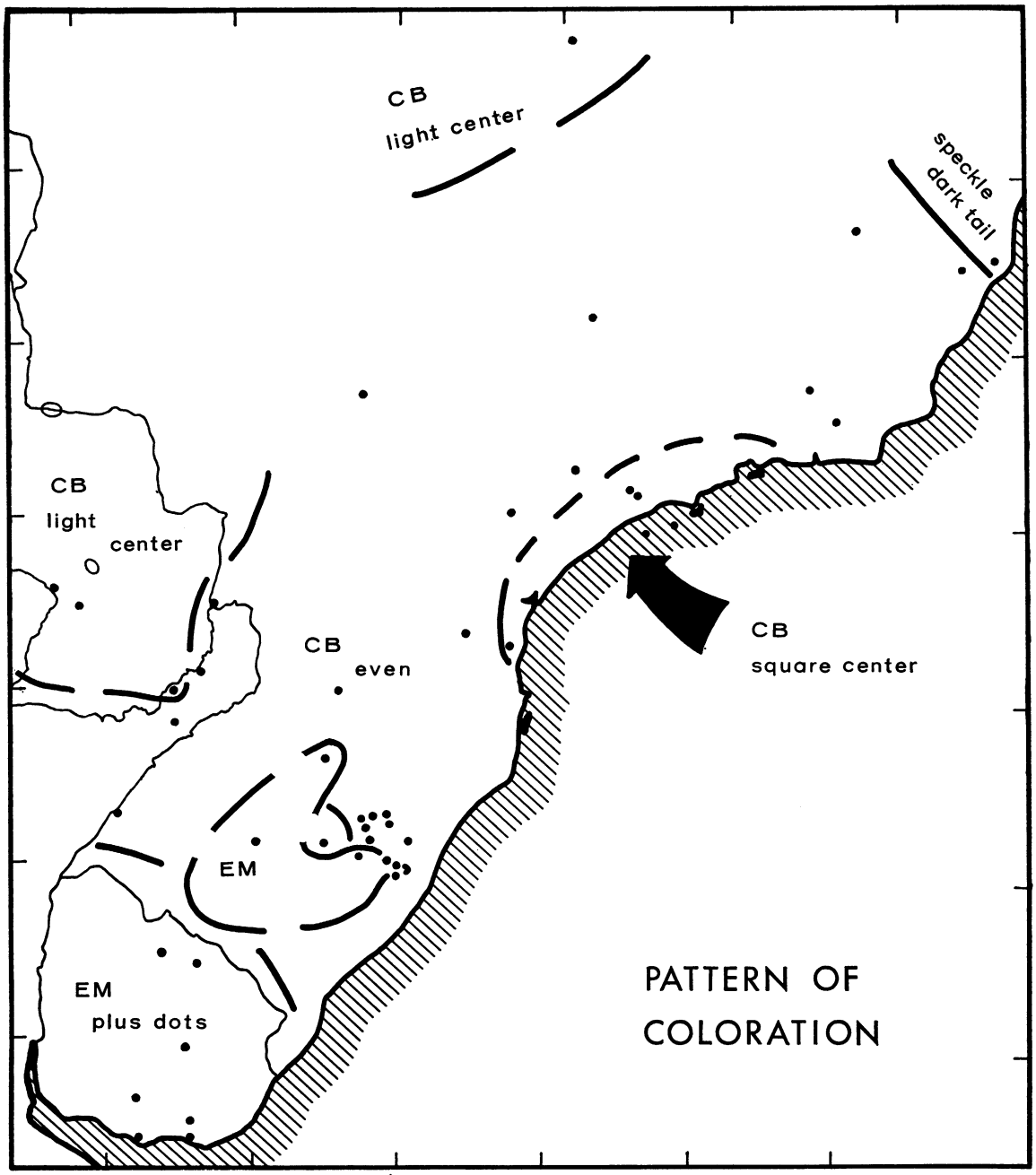


FIG. 25. *Amphisbaena*. Distribution pattern of the various color arrangements. EM stands for edge marking, i.e., the "Viamão" pattern, CB for checkerboard, i.e., the "Coco" pattern and its variants. Details as given in legend to figure 21.

variation in the opposite direction; this material is clearly closest to "Coco."

The specimen from Rio Negro is so soft that it is almost useless, and the individual

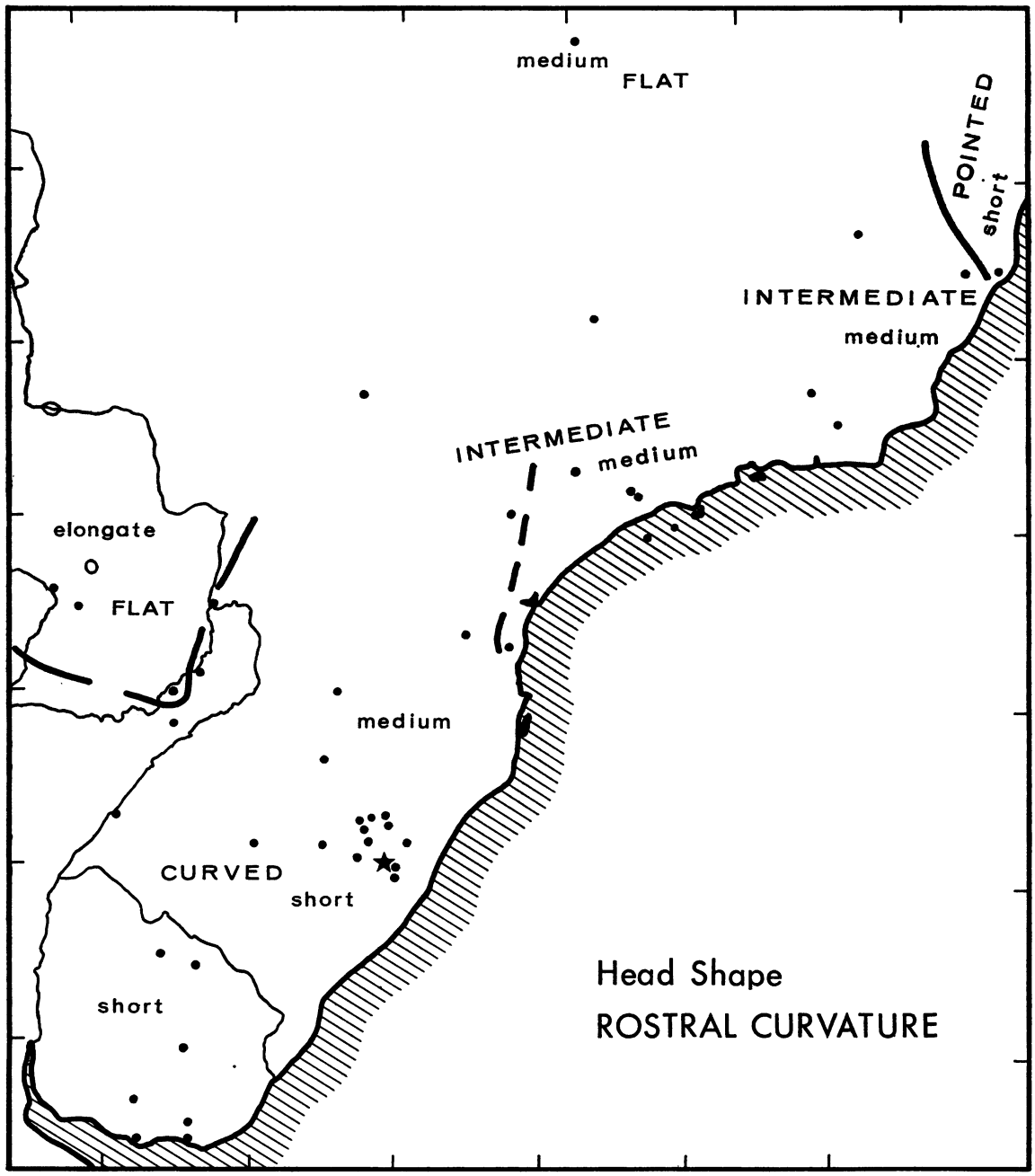


FIG. 26. *Amphisbaena*. Distribution pattern of the various characteristic head lengths and shapes and of the several degrees of rostral curvature. Details as given in legend to figure 21.

from Piraí was not available when this report was written. Notes on the latter suggest that it is closest to the isolated specimens from central São Paulo with which it has been grouped for discussion. The single specimen from Joinville shows equivalent similarities to, and is discussed with, specimens from the eastern and island areas of São Paulo and Rio de Janeiro.

COMPARISONS WITH INLAND SÃO PAULO

AND COASTAL ISLANDS: Material from São Paulo appears to fall into two groupings. The Coastal one includes the specimens from Itapeva, Boituva, São Paulo, and São Bernardo. The individual from Joinville (Santa Catarina) probably belongs to this group.

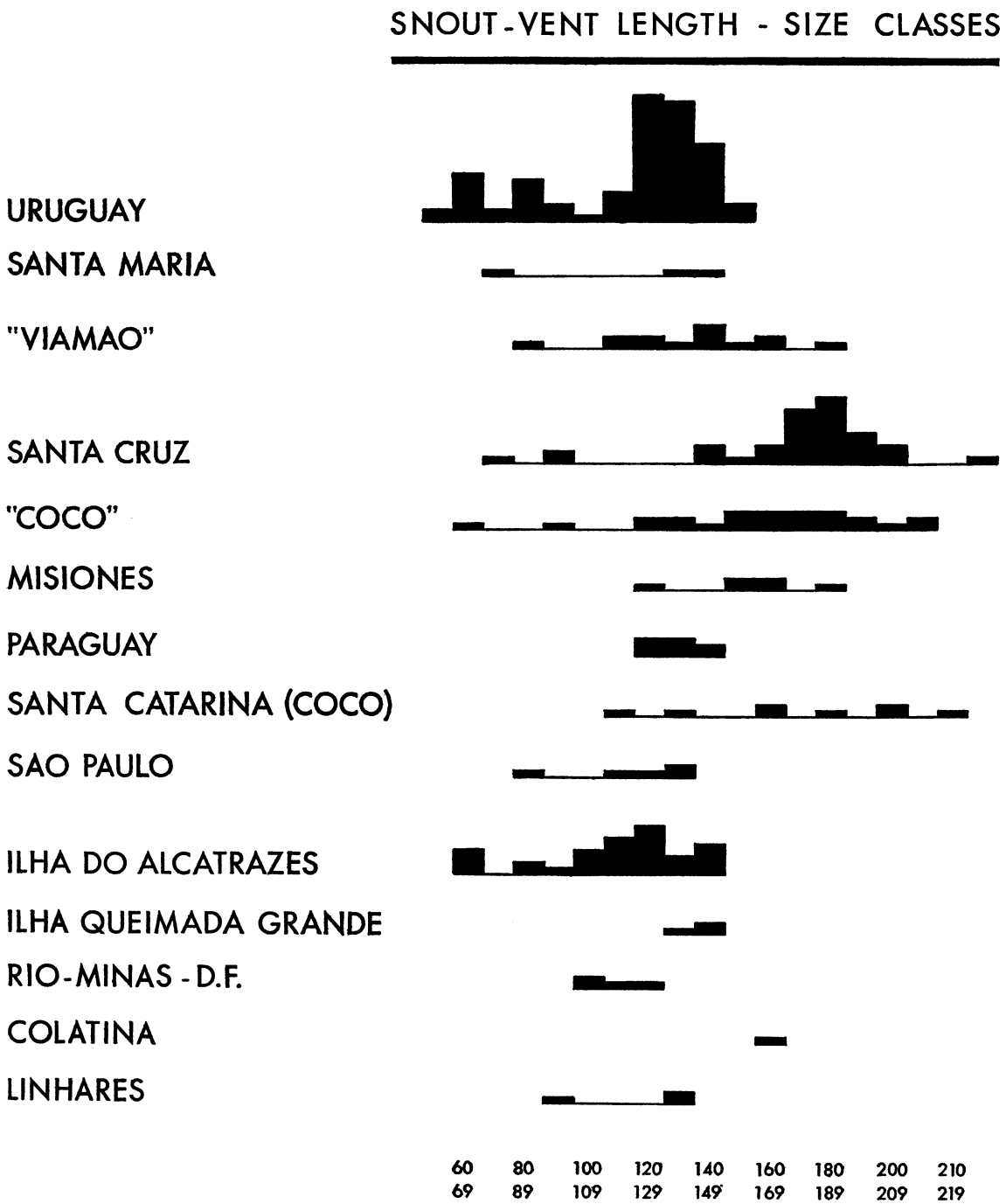


FIG. 27. *Amphisbaena*. Histogram for snout-to-vent length for the several samples. The smallest vertical unit stands for a single specimen.

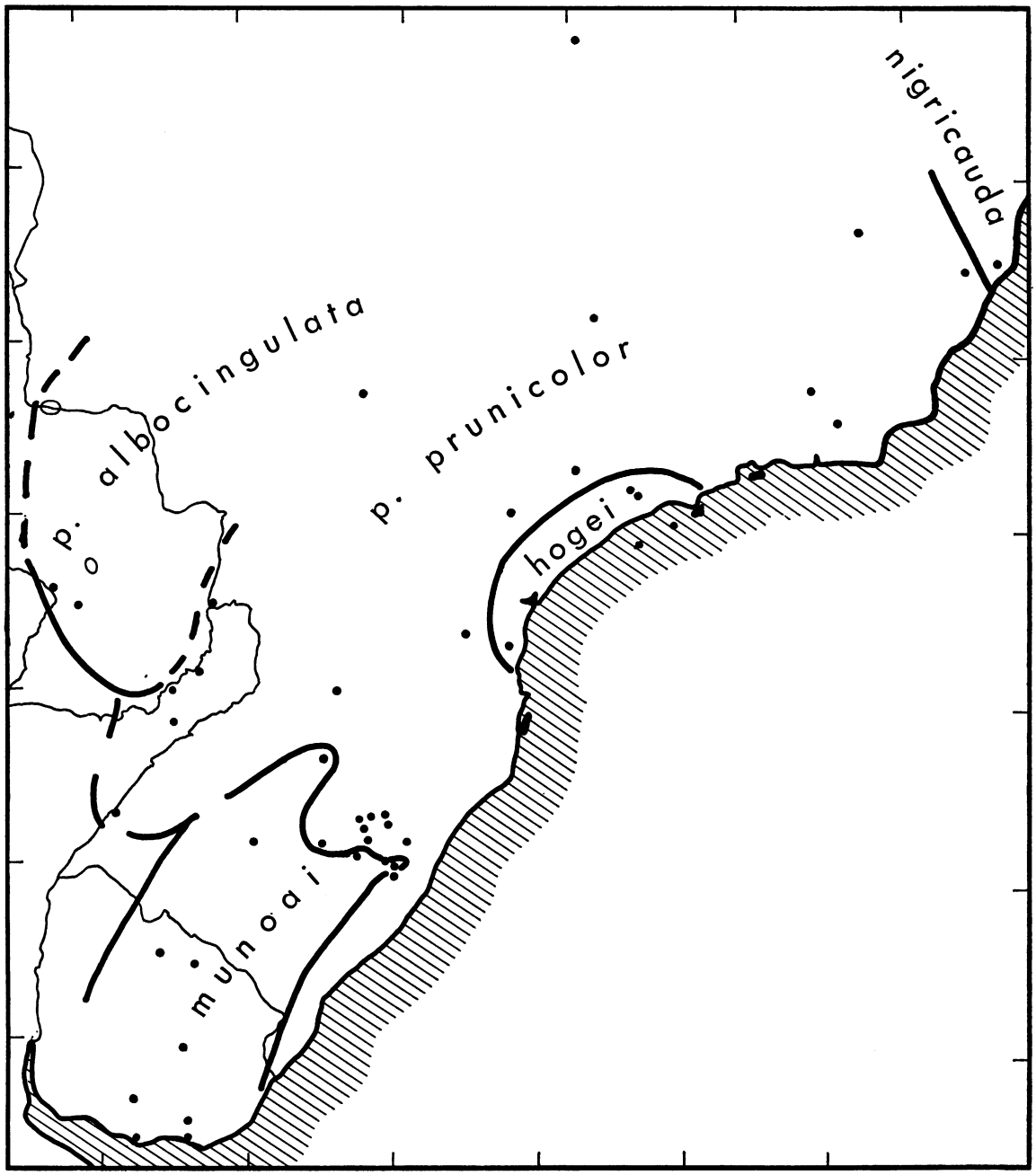


FIG. 28. *Amphisbaena*. Distribution pattern of the several named forms included in the *low* samples.

The second grouping, which is very poorly represented, may include the localities of Franca and Santo Anastacio and perhaps the Piraí (Paraná) record as well. Actually, the Inland records are far too few for one to make any definitive statement of the relationships of the form (or forms) from which they may have been sampled.

The Coastal samples and the specimens from the Ilha de Alcatrazes and Ilha Queimada Grande are characterized by a light brown color pattern. The color is produced by a denser pigmentation of the rectangular center of each dorsal segment, fringed by a nar-

row lighter area. The light margin increases in size in the four to six segments below each lateral sulcus, after which the pigmentation drops out by segments along a more or less continuous line. The ventral surface of the tail is often, but more lightly, pigmented. The head is relatively short. There is a faint protruding ridge near the prefrontal-frontal suture; the snout is ordinarily neither produced nor curved. Two and one-half body annuli participate in the formation of the enlarged nuchal segments which cover the very much swollen temporal masses. Many specimens, particularly from the island samples, lack a second postgenial row. The values for body annuli overlap the range of those of the "Coco" sample, but their mean is much lower. The range for number of caudal annuli overlaps that of the "Viamão" sample, but is also significantly lower. The grouping has by far the lowest autotomy site, and shows no overlap with those of any other specimens. Only the individuals from Itaqui and Misiones approach the upper range limit in this character.

The number of segments to a midbody annulus has slightly lower range limits and means but the difference is statistical and cannot be used for the assigning of individual specimens. The specimens are by far the smallest of any of the forms considered thus far. Their relative tail length is lower, but their relative body diameter is greater even than that of the "Coco" specimens. The distal portion of the tail retains its full diameter (it may even be swollen). The extreme caudal tip is symmetrical, but the entire distal postautotomy section may show some smooth downward curvature.

There is some diversity. The specimens from the two islands show different sample means, but there is no regularity, and, for instance, the São Paulo specimens are in excellent agreement with those from the islands. The entire grouping shows marked differences from both "Coco" and "Viamão."

The specimens from the Inland localities differ by having a "Coco" color pattern (based on the only two adequately preserved individuals). Specimens have a relatively high number of body annuli and tend toward higher numbers of caudal segments as well as toward a higher value for the autotomy site (some "Coco" specimens similarly show such a value). They may also have slightly longer tails and a smaller body diameter, but the samples are inadequate for one to comment on these items. The entire concatenation of characters suggests a resemblance to the "Coco" material; this suggestion remains to be tested.

COMPARISONS OF NORTHERN RECORDS: The maps of the character pattern (figs. 21–27) indicate a series of scattered northern localities from which individual specimens are available. They also show better than any description the lack of pattern to the characteristics of the "grouping." In general, the characteristics resemble the Inland ones, though a few specimens seem closer to the material from Paraguay.

Noteworthy is a series of three specimens from Linhares (Espirito Santo) which differ from everything else in numerous important characteristics. Most important of these is a wedge-shaped head with a prognathous upper jaw, and a small, deeply countersunk lower jaw. The postmental is much smaller than in any of the specimens considered, and the mental and infralabials are correspondingly longer. There are two rows of postgenials and no postmalars; three complete annuli participate in the formation of the enlarged nuchal shields. The numbers of segments to a midbody annulus are very low for both the dorsal and the ventral series. The specimens seem slightly larger than those from any portion of the northern range of *low* material. Relative tail lengths are equal to or slightly shorter than those in these northern specimens, and the midbody diameter is slightly smaller than that in the northern samples. The specimens from Linhares thus appear markedly distinct.

SUMMARY OF VARIATION: The pattern elicited is one of three widely distributed forms, plus a single locality for a fourth one. The single specimen from the Argentine "Chaco" may represent a fifth one, but it does not seem useful to consider it further in this paper.

The first grouping is represented by the "Viamão" sample. The group continues southward to include the sample from Santa Maria and the slightly different, but presumably conspecific, Uruguayan materials. Their differences are not particularly distinct; they are associated with a hiatus in the range and there is no evidence that the range may not

be continuous.

The second grouping includes the "Coco" specimens, the slightly divergent sample from Santa Cruz, the specimens from Misiones (Argentina), as well as the records from inland Santa Catarina and Paraná, from São Paulo and Espirito Santo.

The specimens from Paraguay appear distinct but are probably quite closely related to the preceding assembly, as suggested by the intermediacy of some of the individuals from Misiones. Also in favor of this view is the character pattern of the specimens from Minas Gerais and Brasilia. The scarcity of specimens from the critical inland and northern zones does not permit a decision as to whether these two forms occupy parallel north-south ranges, or if the general intermediacy of the northern materials implies a different explanation.

The materials from coastal Santa Catarina and São Paulo and from the islands of Alcatrazes and Queimada Grande represent the third grouping. They are quite distinct from the materials from surrounding areas; to the south they differ almost equally from the specimens of the "Viamão" and "Coco" samples.

The fourth grouping includes only the specimens from Linhares.

TAXONOMIC ASSIGNMENTS: Two basic patterns may now be established. In both, the Linhares specimens must be recognized as a distinct species. However, the remaining materials may be considered either to represent four races of a single species, or three full species that seem generally allopatric and perhaps replace one another.

The discrimination between the "Viamão" and "Coco" samples is fundamental to the entire issue. The expansion of the comparison did not indicate any additional sites of sympatry, nor did it show any breakdown of the intersample differences. The sample from Santa Cruz is geographically intermediate and generally similar to the "Coco" sample, yet where it differs from this it departs from the "Viamão" pattern as often as it approaches it. It is also possible to assume that the intermediacy of some characteristics of the single specimen from Itaqui defines the gene-exchange zone between two otherwise separated groups of races, but such an explanation is neither the simplest nor the most probable. The rostral curvature of the southern populations and the over-all similarity of many characters are perhaps the strongest argument for conspecificity, but these can be explained on the basis of similar selective influences that acted on similar genetic backgrounds. The two assemblages are for the time being considered to be distinct species.

The assignment of the São Paulo grouping is perhaps more uncertain. In some ways it is intermediate between the "Coco" and "Viamão" patterns, but this intermediacy does not mean much in view of the extensive geographic separation and the existence of several characters that depart markedly from the character patterns of both of these forms. The evidence is admittedly weak, but treatment as a full species appears the most logical decision derivable from the evidence.

All the three major groupings might be split further. From the "Viamão" sampling, one may separate the Uruguayan and Brazilian specimens. From the "Coco" sampling, the Paraguayan populations are certainly distinct; the intermediate specimens are few and come from localities that are sharply restricted geographically. The sample from Santa Cruz is less distinct. The northern populations of "Coco" pattern may also prove to show differences, but these are obscure and appear to be of considerably less magnitude. The populations of the third form from the two coastal islands show differences from one another and from the mainland specimens. These differences, however, appear relatively minor, particularly when one considers the astonishing fact that there are no records of the form from the coastal plain proper. The presence of several cases of well-marked differences, assignable to and constant within forms inhabiting major fractions of the range, then lends additional weight to the hypothesis that these are indeed good species.

Although several of the species appear to be polytypic, I here choose to name only the Paraguayan population, which is clearly the most distinctive. Nomenclatorial recognition of additional populations might well follow rather than precede more detailed studies of the ecological pattern underlying the variability of the several species.

ATTRIBUTION OF NAMES

In 1839 Duméril and Bibron (p. 490) described the new species *Amphisbaena darwinii* on the basis of specimens brought from "Montevideo" by M. d'Orbigny. They indicated in the description that they had also seen numerous other individuals of this species collected at the same site which were then in the Charles Darwin collection. They did not select a type. The collection of the Muséum National d'Histoire Naturelle in Paris retains only three specimens (all from Montevideo) that are pertinent to the issue. One of these (M.H.N.P. No. A-3107) was collected by M. d'Orbigny; the other two (M.H.N.P. Nos. A-3112, A-3113) were collected by Charles Darwin. All three specimens are in good agreement with the description. They share the *high* character pattern.

The d'Orbigny specimen is severely damaged. The skin and soft tissues of the head have been removed to expose the skull and anterior vertebrae. It is thoroughly rotten at two places along the trunk, and has a tail that has broken (and the tip lost) postmortem. The other two specimens are in better condition. The original discussion is vague enough to permit us to consider all of these as syntypes. I here choose specimen M.H.N.P. No. A-3112 as the lectotype, as it is the largest and the best preserved of the series, and its body proportions closely fit those given in the original description. The name *darwini* then applies to the south Uruguayan subspecies of the *high* form.

The rare "Reise durch die La Plata-Staaten" of Hermann Burmeister contains the description of *Amphisbaena heterozonata* (1861, vol. 2, p. 527), initially referred to as *Lepidosternon heterozonatum* (1861, vol. 1, p. 309). The composite description mentions 170 to 180 body annuli, 18[1] caudal annuli, of which the last 10 were the longest, four precloacal pores (absent from juveniles), and a dotted coloration. The first mention referred to specimens taken "bei Mendoza"; the later description amplified this to "bei Mendoza und Tucuman."

Two syntypes were deposited in the Halle University collection (Strauch, 1881, col. 79; Lorenz Müller, 1941, p. 195). Müller, who examined them shortly before the collection was destroyed (H. Wermuth, personal communication), found the counts of Burmeister and Strauch (199, 203) too low and recorded 201 and 204 body annuli, 17 caudal annuli, and 16 dorsal and 18 ventral segments to a body annulus. He also restricted the type locality to "Mendoza."

The description leaves little doubt that the specimens were sampled from west Argentinian populations of the *high* character pattern. They do not differ from these in any significant aspect. Since this assemblage does not reach Mendoza (the collection in the Instituto de Biologia of that city lacks any representation of it from that state), it is necessary to change the type locality to Tucumán, by present action. The name *A. darwini heterozonata* then applies to the Argentine assemblage of the *high* form (though it may have to be restricted to an extreme western assemblage, if such should ever be characterized).

In 1878 Peters described and illustrated four new species of *Amphisbaena* and gave the first illustrations of several previously described, but never illustrated, forms. He presented a description (p. 779) of the new species *A. mildei* on the basis of a single specimen from "Porto Alegre," and compared the specimen only with *A. darwini*, of which he illustrated one of the typical specimens in the Paris Museum, claiming that it differed drastically from the latter form in the head scalation. The major aspect in which the illustration of head segmentation furnished by him differed from the latter is that the prefrontals are somewhat more elongate and that sutures divide the second and third supralabials (asymmetrically to judge from his description, p. 780).

The holotype (Z.M.U. No. 6255) appears to have been lost when the collections were moved from storage after the war (H. Wermuth, *in litt.*). The pertinent portions of the original description indicate that the occipital and temporal regions were covered with small, quadrangular segments, that

[1] Counting methods have differed among authors.

there were four poorly visible precloacal pores and six precloacal segments, and that there were 198 body annuli and 24 caudal annuli. The snout to vent, plus tail, length was 293 +37 mm., and the trunk diameter 11 mm. The color was described as violet-brown dorsally and white ventrally. The description lacks statements regarding the number of segments to a midbody annulus and any comments regarding the condition of the caudal tip. The latter omission is particularly vexing as the individual was of adult size.

The presence of small quadrangular shields on the nape, and the body proportions combined with the faintness of the precloacal pores, suggest that the specimen was sampled from the *high* assemblage; none of the other characters, except for the split supralabials and high number of caudals, would suggest that such is not the case. The asymmetry of supralabial splitting may indicate that the specimen was anomalous. In any case, it is impossible to assign it definitely to one of the three geographical groupings that could have been sampled by someone collecting from "Pôrto Alegre." Since the type appears to have been lost and the concept of the form is unclear, the name may be considered a *nomen oblitum* (Stoll, 1961, art. 23b).[1] In the present century it has been cited only five times, twice in lists without comment (Goeldi, 1902; Burt and Burt, 1933), and in synonymy also without comment (Amaral, 1935).

In 1885 Cope presented a key to the species and genera of amphisbaenids in a paper in which he described two new amphisbaenids collected by Herbert H. Smith in Rio Grande do Sul. He mentioned that the "principal collections were made at Sao Joao do Monte Negro," and this site has been accepted as the type locality of the forms described by him (Vanzolini, 1953, p. 124).

The first of these species is *A. trachura*. Its holotype is still in the collection of the Academy of Natural Sciences of Philadelphia and was available for the present study. It is in good agreement with Cope's description, and possesses marked caudal tuberculation which is described and illustrated in Cope's report. Nevertheless Boulenger (1885b, p. 297) later the same year relegated this name to the synonymy of *darwini* as "merely an individual anomaly."

The characteristics of the type indicate that it was sampled from the northern portion of the range of the *high* form. It is not certain, however, that the specimen was actually taken at Montenegro, since recent collecting there (by the present author) turned up numerous individuals of *Anops*, but none of *Amphisbaena*. Since the name has recently been cited by Vanzolini (1953, MS), it remains available, and this population should then be characterized as *A. darwini trachura*.

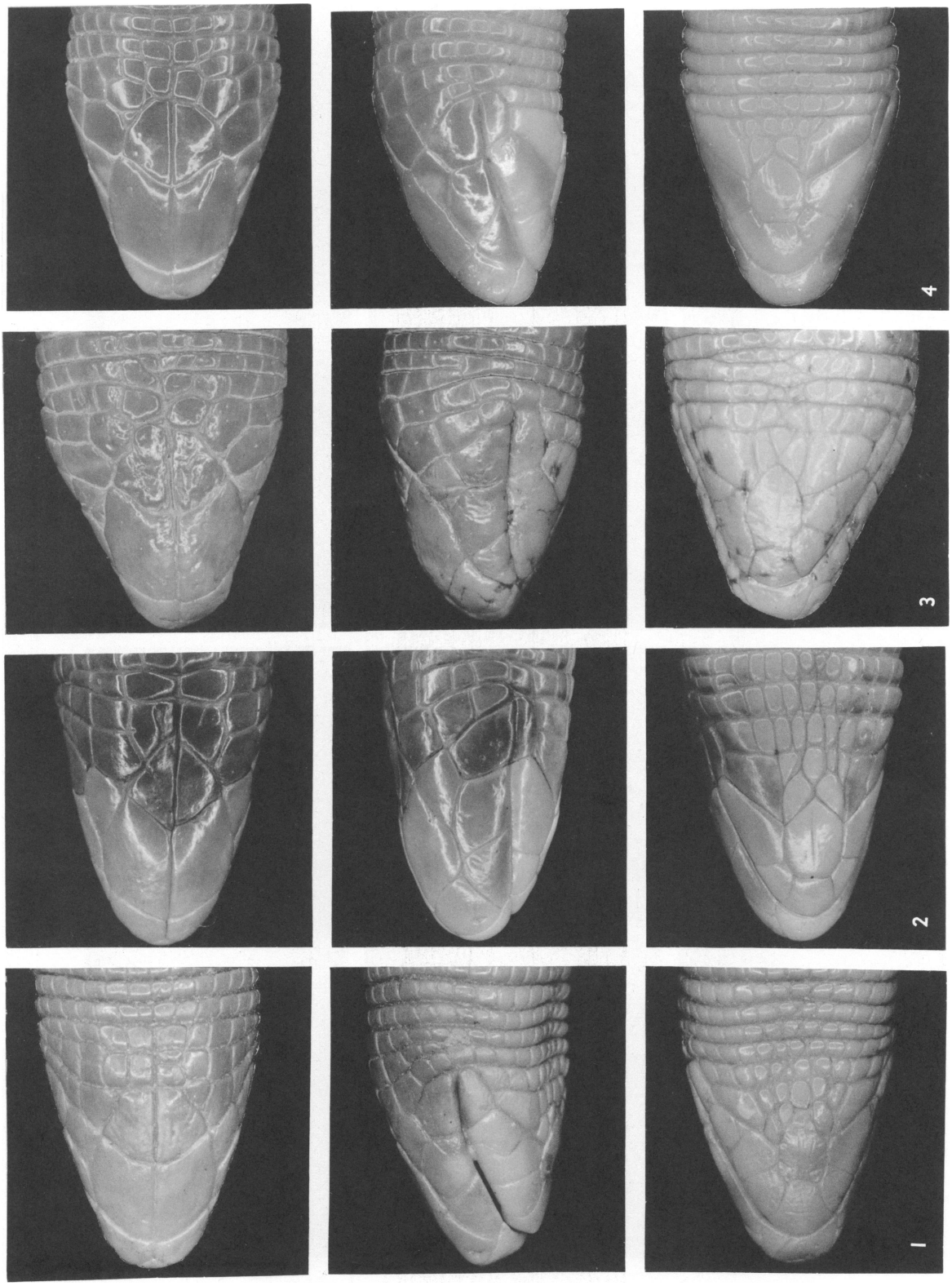
Cope, in the same paper (1885, p. 189, figs. 5a-d), also described and illustrated the new genus and species *Aporarchus prunicolor* from the same collection and type locality. The holotype, which was available for these studies, is still in the collection of the Academy of Natural Sciences of Philadelphia, in a state of adequate preservation, and in good agreement with Cope's description. Cope's emphasis on the absence of precloacal pores in his generic diagnosis apparently led Boulenger (1885b, p. 297) to synonymize this form with *A. darwini*, a decision adopted by most authors. The name applies to the "Coco" assemblage.

In the same year Boettger (1885, p. 7) reported on a collection made in Paraguay by H. Rohde from which he described *Amphisbaena albocingulata* and four new species of *Leposternon*. The new *Amphisbaena*, the type of which was then in an Institute "Linnaea," was characterized mainly by the presence of a unilaterally split ocular and of a split pair of "frontonasorostrals." The coloration was supposed to be a lighter brown than that of *A. darwini*, and the specimen showed a light-colored precloacal region. Boettger also reported on six specimens of "*A. darwini*" from the same source; the composite description of the entire series suggests that he had an anomalous specimen of the *low* grouping from Paraguay, specimens of which often show this particular coloration. The name is then available for that grouping.

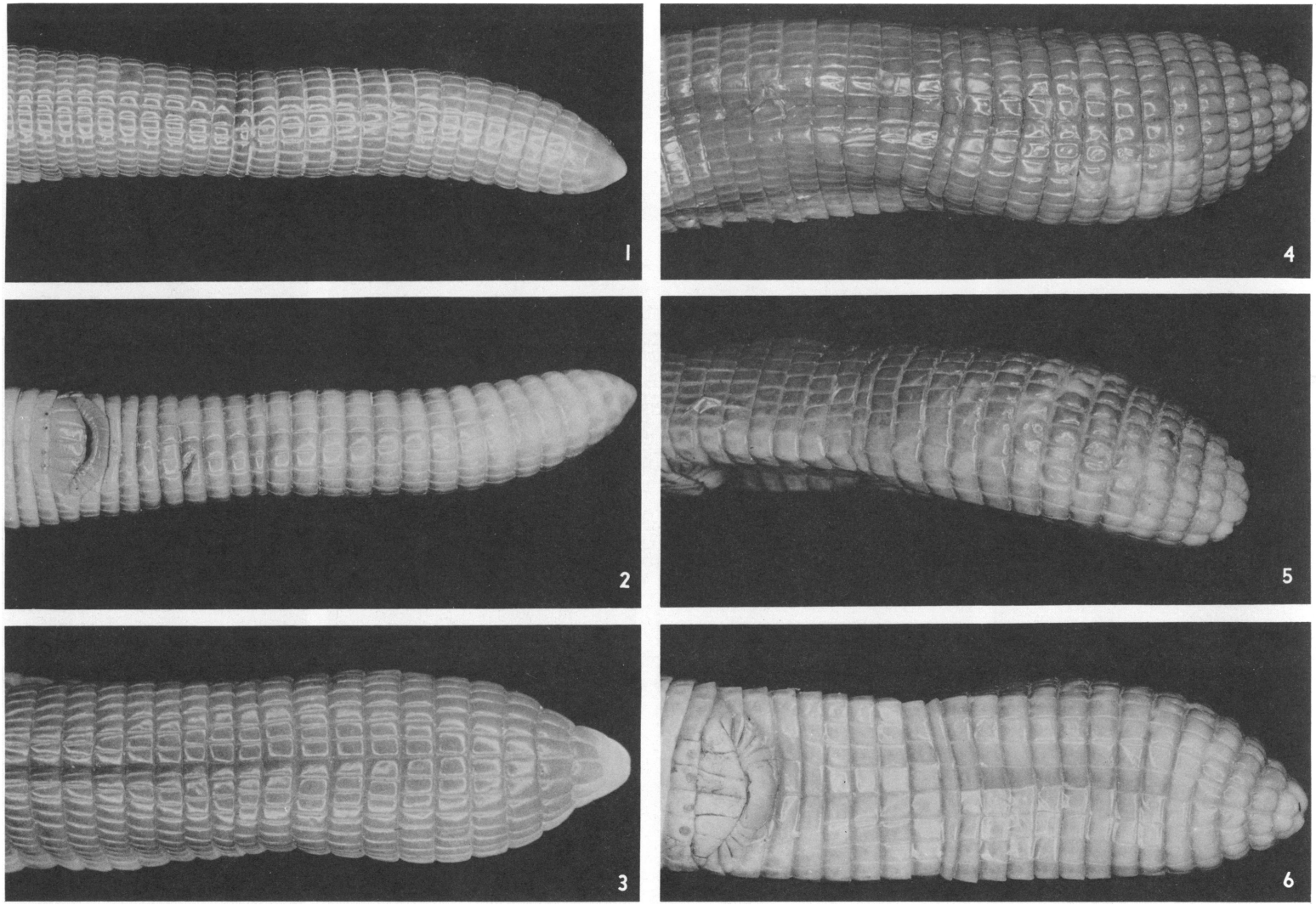
There is now no record of a "Naturhistorisches Institut Linnaea in Frankfurt a. M." The courtesy of Dr. H. W. Parker, who

[1] Since the *nomen oblitum* rule has been temporarily suspended, I have proposed that the name be suppressed (Gans, in press).

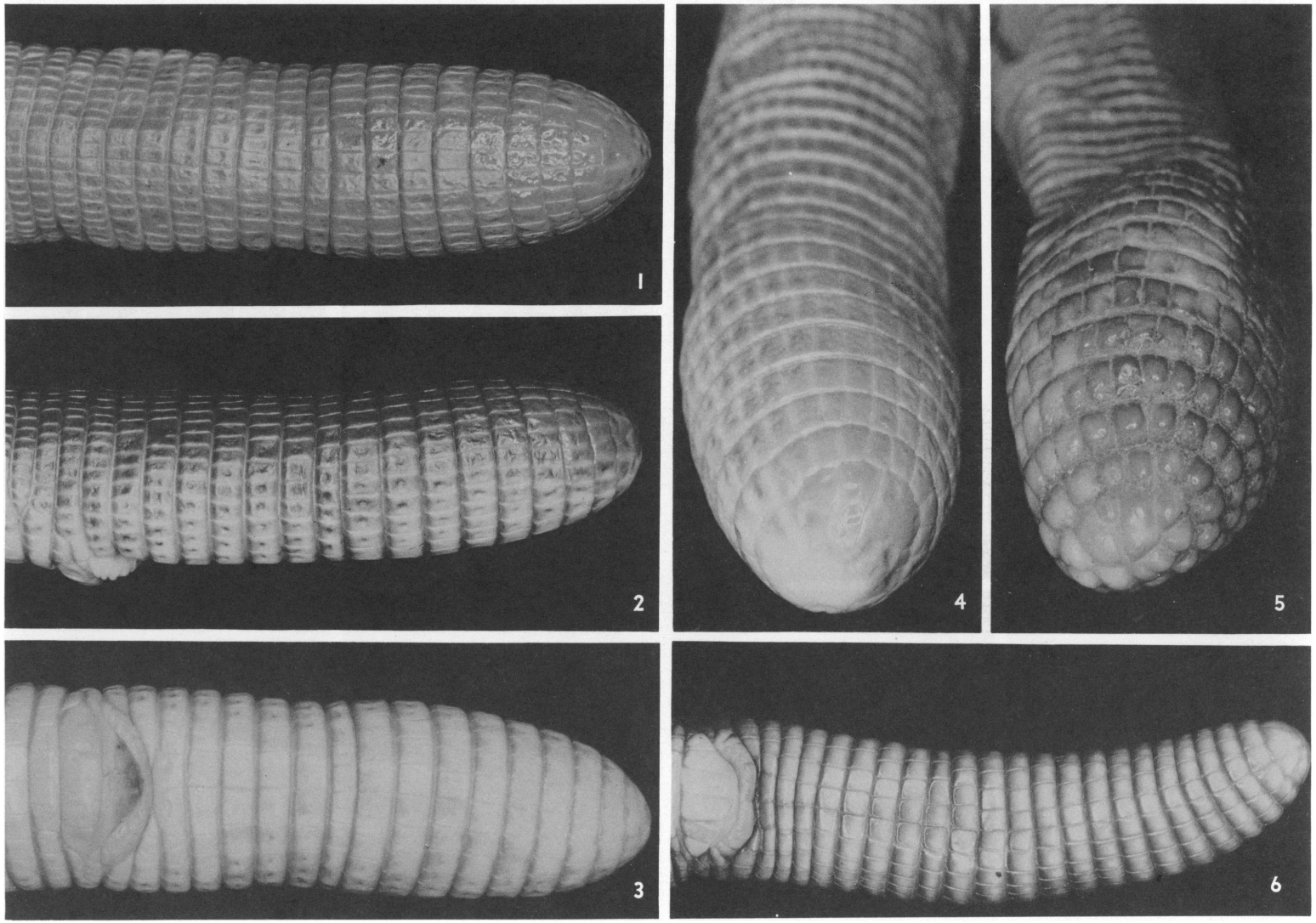
PLATES 37–45



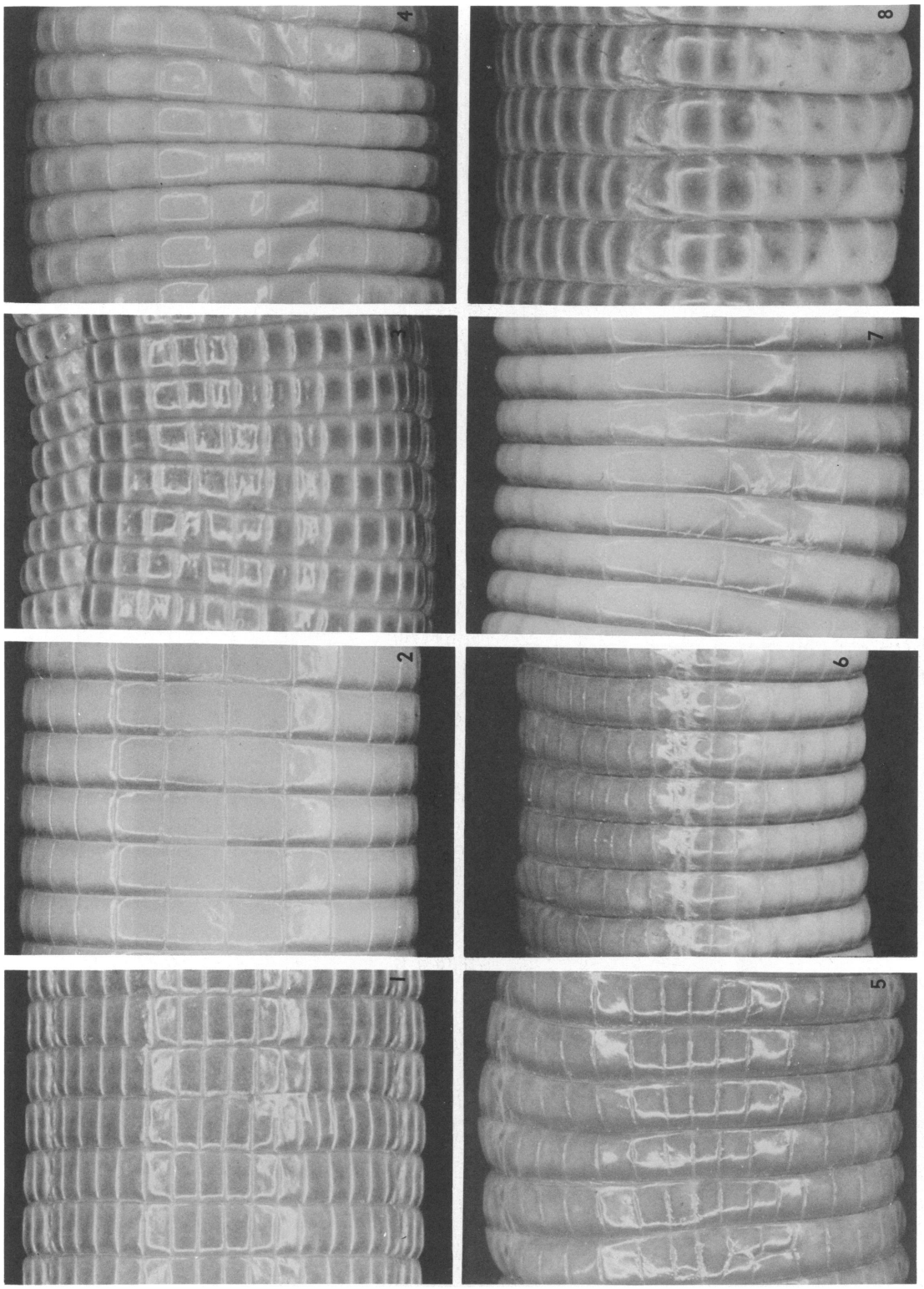
Amphisbaena darwini, dorsal, lateral, and ventral views of head. 1. *A. darwini darwini*, C.G. No. 2208, from Montevideo (Colón), Uruguay. 2. *A. darwini trachura* (lead phase), M.R.C.N. No. 2043, from São Francisco de Paula, Rio Grande do Sul, Brazil. 3. *A. darwini trachura*, D.Z. No. 6516, from Castro, Paraná, Brazil. 4. *A. darwini heterozonata*, Z.S.M. No. 1-A, from Estancia La Germania, Santa Fé, Argentina



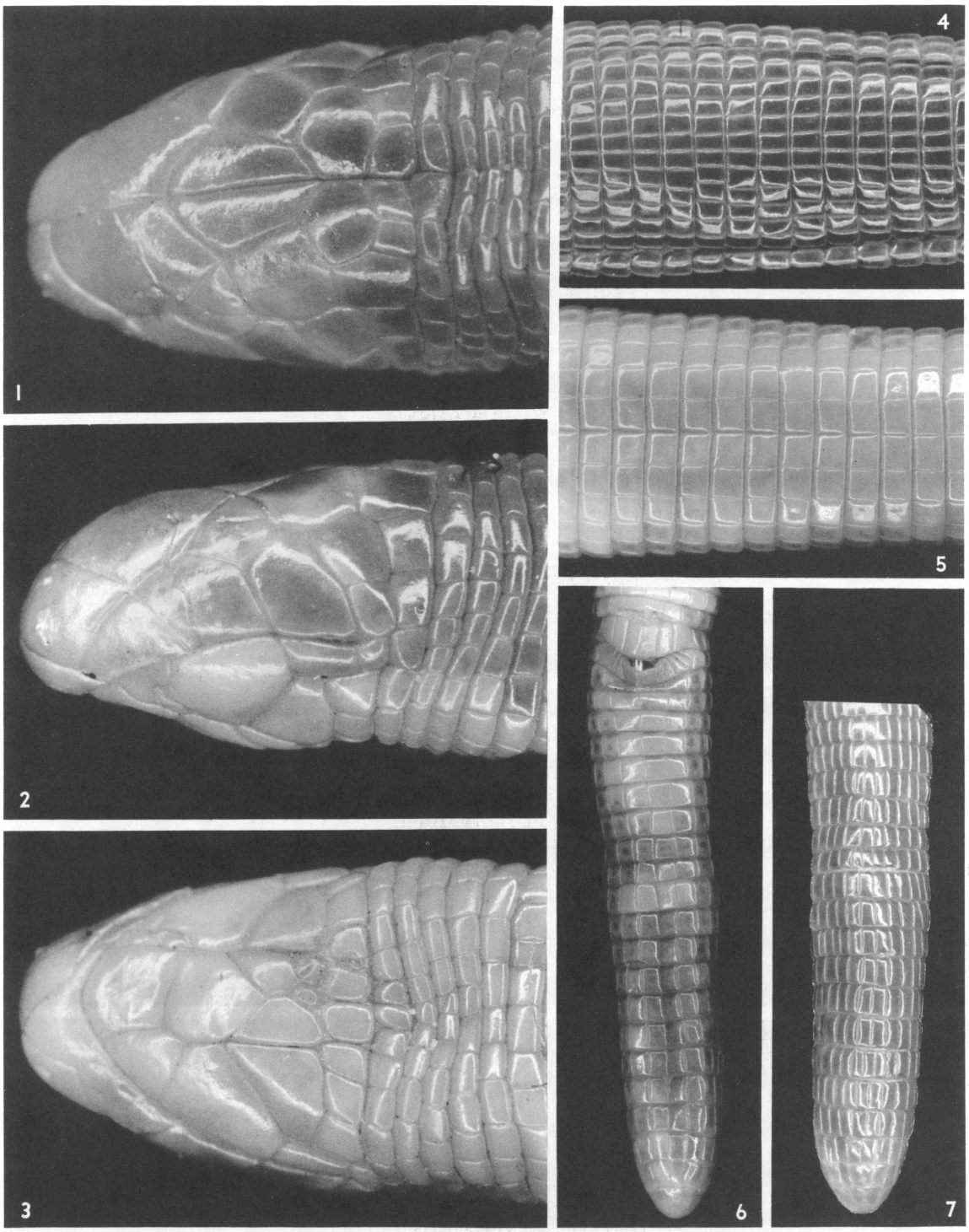
Amphisbaena darwini, views of tail. 1, 2. *A. darwini darwini*, dorsal and ventral views of B.Y.U. No. 16131, from Montevideo, Uruguay. 3–6. *A. darwini trachura*. 3. Dorsal view of M.R.C.N. No. 2279, juvenile from Canoas, Rio Grande do Sul, Brazil. Note smooth segments and nature of distal tip. 4–6. Dorsal, lateral, and ventral views of D.Z. No. 6665 from Texeira Soares, Paraná, Brazil



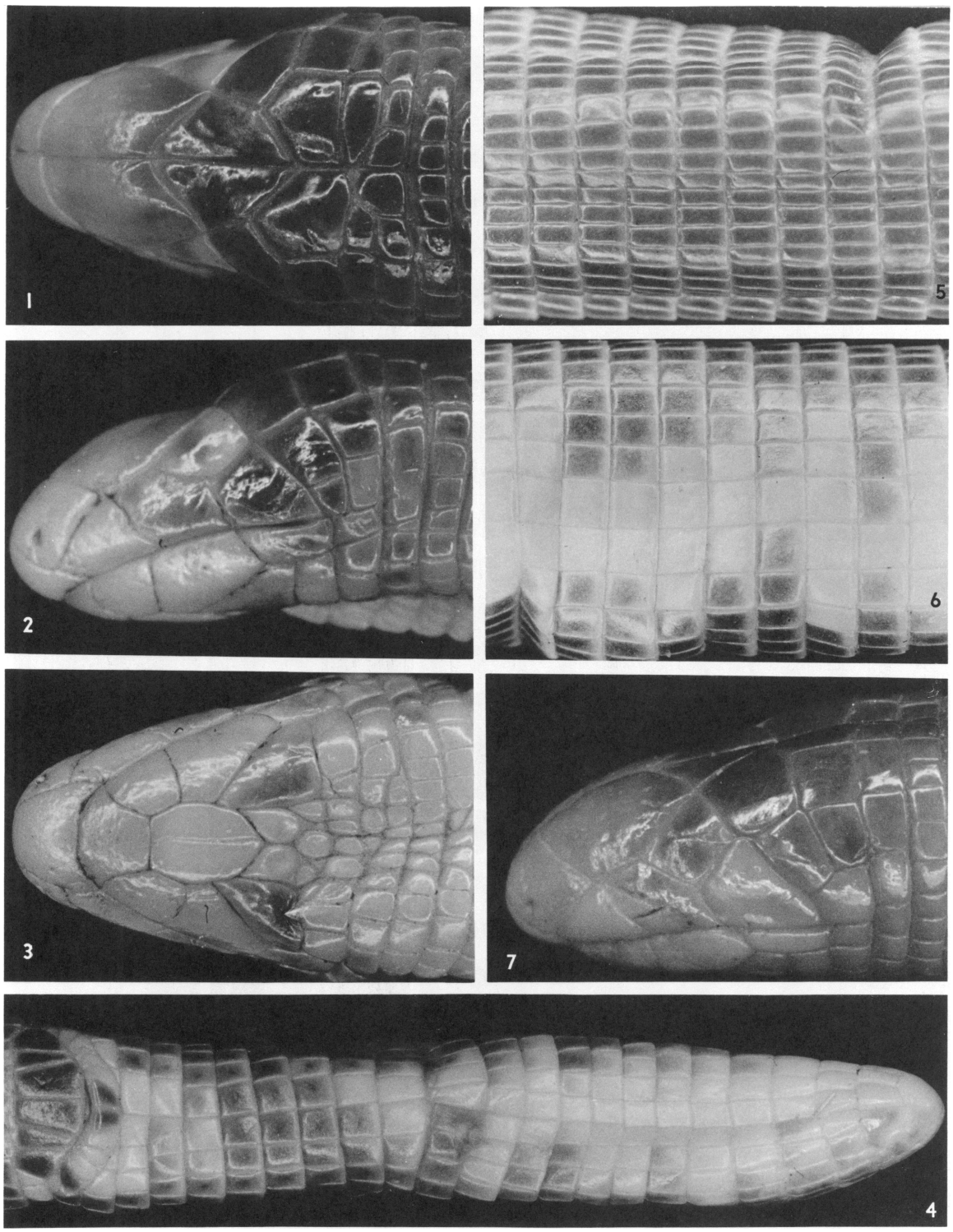
Amphisbaena darwini, views of tail. 1–4. *A. darwini heterozonata*, dorsal, lateral, and ventral views, and caudal tip of L.I.H.U.B.A. No. 247, from Iraola, Parque Perevra, Buenos Aires, Argentina. 5. *A. darwini trachura*, caudal tip of D.Z. No. 6665, from Texeira Soares, Paraná, Brazil. Note marked tuberculation. 6. *A. darwini darwini*, ventral view of M.R.C.N. No. 1432, from São Francisco de Paula, Rio Grande do Sul, Brazil



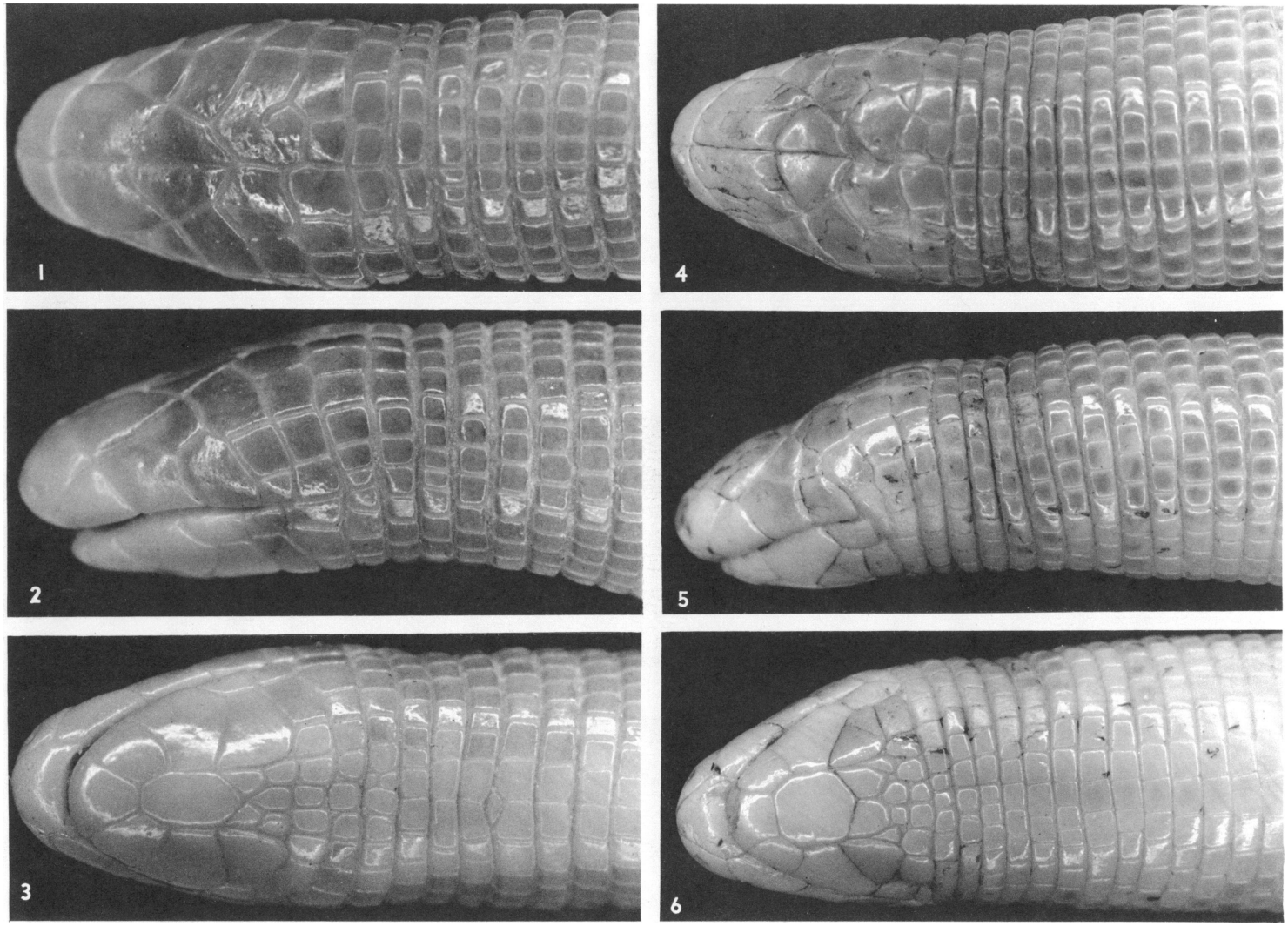
Amphisbaena darwini, midbody views. 1, 2. *A. darwini darwini*, dorsal and ventral views of M.N.H.M. No. 581, from Montevideo, Uruguay. 3–7. *A. darwini trachura*. 3, 4. Dorsal and ventral views of N.M.W. No. 12337:2, from Joinville, Santa Catarina, Brazil. 5–7. Dorsal, lateral and ventral views of M.R.C.N. No. 2042, from São Francisco de Paula, Rio Grande do Sul, Brazil. Note edge marking. 8. *A. darwini heterozonata*, lateral view of M.A.C.N. No. 2791, from Tandil ("Sierra, cerca à la ciudad"), Buenos Aires, Argentina. Note edge marking and central pigment emphasis



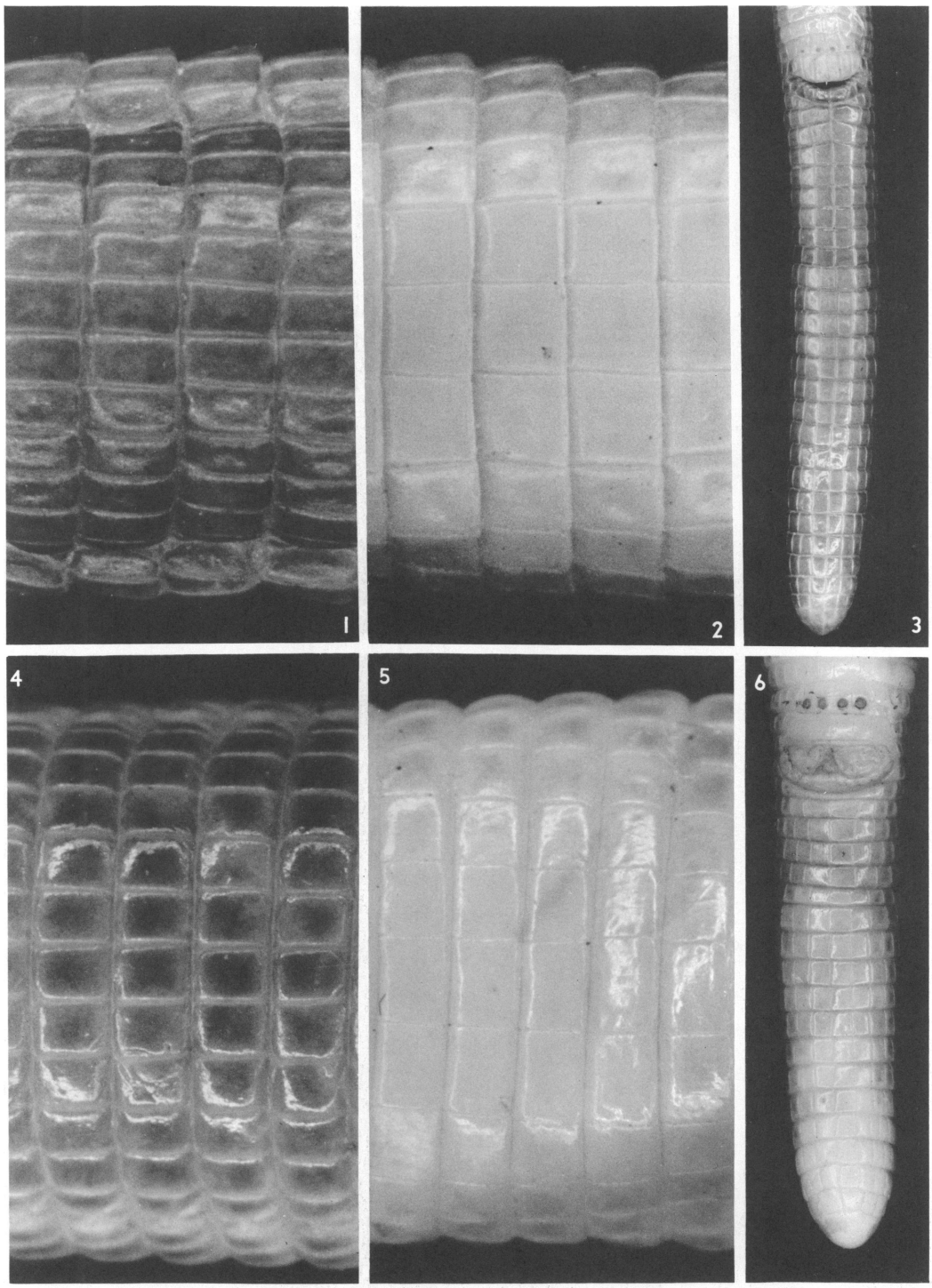
Amphisbaena munoai from Piriapolis, Cerro San Antonio, Maldonado, Uruguay. 1–3. Dorsal, lateral, and ventral head views of C.G. No. 2195. Note prefrontal protrusion. 4, 5. Dorsal and ventral views at midbody of C.G. No. 2197. 6, 7. Dorsal and ventral views of cloaca and tail of C.G. No. 2196



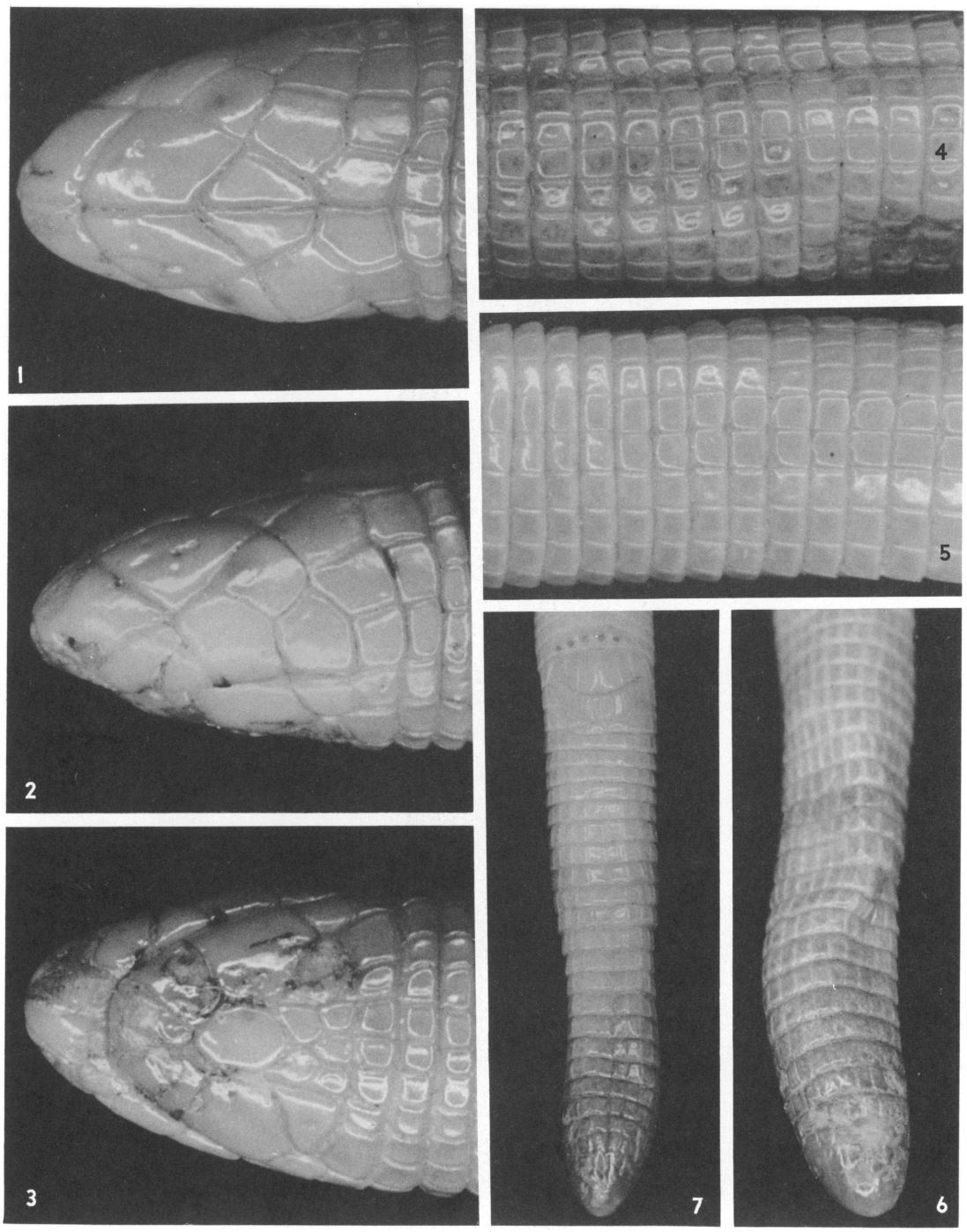
Amphisbaena prunicolor prunicolor. 1–3. Dorsal, lateral, and ventral views of head of D.Z. No. 6389, from Morro do Coco, Rio Grande do Sul, Brazil. 4. Ventral view of tail. 5, 6. Dorsal and ventral views at midbody of same specimen. 7. *A. munoai*, lateral view of head of M.R.C.N. No. 1182, from Viamão, Rio Grande do Sul, Brazil



Amphisbaena, head views. 1–3. *A. prunicolor albocingulata*, dorsal, lateral, and ventral views of head of I.M.Z.U.T. No. 985, from Asunción, Paraguay. 4–6. *A. hogei*, dorsal, lateral, and ventral views of head of S.M.F. No. 57909, from Ilha Queimada Grande, São Paulo, Brazil



Amphisbaena, midbody and caudal views. 1–3. *A. prunicolor albocingulata*, I.M.Z.U.T. No. 985, from Asunción, Paraguay. 1, 2. Dorsal and ventral views at midbody. Note lightening of centers of dorsal segments. 3. Ventral view of cloaca and tail. 4–6. *A. hogei*, S.M.F. No. 57909, from Ilha Queimada Grande, São Paulo, Brazil. 4, 5. Dorsal and ventral views of midbody. 6. Ventral view of cloaca and tail



Amphisbaena nigricauda, from Refugio Sooretama, Linhares, Espirito Santo, Brazil. 1–3. Dorsal, lateral, and ventral views of head of M.N. No. R3305. 4, 5. Dorsal and ventral midbody views of C.G. No. 3207. 6, 7. Dorsal and ventral views of tail of C.G. No. 3207

checked the archives of the British Museum (Natural History), elicited the information that the Institute had been a commercial trading concern. Apparently it purchased collections, arranged for them to be determined by specialists (in this case by Boettger), and then sold their components to various museums. The Institute seemingly moved to Berlin during 1885 and appears to have gone out of business some time later. One to three specimens of the "*A. darwini*" in the collection were purchased by the Vienna Museum and were available for this study, as was a Berlin Museum specimen marked "*A. albocingulata*," Paraguay, Rohde.

The type appeared initially to have been lost. It, and the types of the four new species of *Leposternon*, were found by accident on the list of the Leningrad collection (Z.I.L.) of amphisbaenids kindly furnished by Dr. I. S. Darevski. Their existence there and the 1885 acquisition date suggest that Strauch purchased the typical material, probably before the publication of Boettger's report, as the prospectus in its introduction offers only the duplicates for sale.

The probable conspecificity of the Coco and Paraguayan samples forces a decision regarding priority of these two names published in the same year. Cope's paper (1885, p. 169) bears the printed inscription "Printed March 7, 1885." Boettger's paper bears only the year of publication. Since the name *albocingulata* appeared in the second half of the volume, it is unlikely that it antedated *prunicolor*, and the Paraguayan population should then be known as *Amphisbaena prunicolor albocingulata*.

In 1950 Vanzolini published the new name *Amphisbaena darwini hogei* in the first of his papers on the group. The typical material, collected on the Ilha dos Alcatrazes, was examined in the Departamento do Zoologia (São Paulo) during the present study. It clearly belongs to the coastal and island *low* pattern form. Vanzolini's differences between the island population and mainland material turn out to be partly spurious; his comparison series, which was not otherwise identified, seems to have been composite.

In 1960 Klappenbach, in a short, well-argued paper, presented evidence for the existence of two sympatric amphisbaenids in Uruguay, namely, *A. darwini* and the then new *A. munoai*. The types of the latter form were examined and belong to the Uruguayan population of *low* character pattern. Some of the paratypes were used in this study. The name is then available for the "Viamão" sample and the Uruguayan population.

No name seems to be available for the new form from Linhares, and the new name *nigricauda* is here proposed for it.

SYSTEMATIC ACCOUNTS

Amphisbaena darwini Duméril and Bibron

This form exhibits very complex geographic variation which is discussed above. Table 3 presents a summary of the major differences between the races and may thus serve *in lieu* of separate diagnoses. The descriptions emphasize non-meristic characters.

The paragraphs on "Locality Records" are placed at the end of the descriptive accounts to facilitate citation of intermediate populations. Localities are cited approximately from south to north. Whereas all specimens that were examined are recorded in these paragraphs, those that lacked data as well as those assigned only to countries or to the state of Rio Grande do Sul were omitted from the raw data, on deposit in the Library of Congress (see p. 191).

Amphisbaena darwini darwini
Duméril and Bibron

Plate 37, figure 1; plate 38, figures 1, 2; plate 39, figure 6; plate 40, figures 1, 2; text figures 6–17, 29, 30

Amphisbaena darwinii DUMÉRIL AND BIBRON, 1839, p. 490. *Terra typica:* "Montevideo," Uruguay. Lectotype: M.H.N.P. No. A3112 (by present action). Lectoparatypes: M.H.N.P. Nos. A3107, A3113.

DESCRIPTION: This form of *Amphisbaena* is medium-sized, in life brownish violet dorsally and pinkish white ventrally, these colors fading to brown dorsally and off-white ventrally in preservatives. The color is expressed evenly across the dorsal segments, with occasional and faint pigment emphasis along the anterior edge or, rarely, in the center of segments. The anterior pigment emphasis (edge marking) is particularly noticeable on the sides of the trunk and on the ventral surface where the edge marking drops out by segments. The lateral countershading, in contrast, occurs by an irregular lightening of pigment area and pigment density. The dorsal surfaces of the head and tail are emphasized by darker, more dense pigmentation. The chin is light, and the light coloration extends across the infralabials onto the mental and rostral, and posteriorly to the cloaca. The third infralabial is often more darkly pigmented, and there may be a ventrad extension of the darker dorsal coloration in the nuchal region. The zone dorsolateral and posterior to the cloaca generally has faint indications of central pigment emphasis.

TABLE 3

COMPARISON OF CHARACTERISTICS FOR THE THREE RACES OF *Amphisbaena darwini*

	darwini	*heterozonata*	*trachura*
Body annuli			
Means	179.5–195.2	191–203	176–201
Ranges	178–199	190–207	168–208
Caudal annuli			
Means	19–22	14–16.2	17–20
Ranges	18–23	13–17	15–22
Segments to a midbody annulus			
Ventrals (ranges)	16.5–22	(15) 17.5–22	17–22.5
Dorsals (ranges)	13–18	14–18.5	14–21
Caudal tip	Smooth	Smooth	Tuberculate
Tail	Long	Short	Medium
Size	Medium	Small	Large
Head shape	Long	Long-medium	Short
Color	Even to faintly dotted; ventral surface generally clear	Dotted (often only on anterior body and tail)	Markedly and entirely dotted (or lead-colored); ventral surface generally pigmented

A light, even color extends across the ventral surface of the tail, generally starting at the second postcloacal annulus; the autotomy annulus is only rarely and slightly emphasized by darker pigmentation.

The head segmentation is characterized by lack of major fusions and by a pair of extremely large, roughly trapezoidal prefrontals, followed by small triangular frontals, their posterior edges irregularly rounded or scalloped. The head is slightly flattened dorsoventrally and generally of oval cross section with a variably downcurving rostral tip. The angle subtended by the sides of the face increases with age, i.e., with emphasis of the temporal musculature. These muscle masses lying over the temporal region are faintly apparent externally. The trunk narrows slightly just posterior to the head and becomes much wider thereafter. It reaches its full width near the level of the twentieth body annulus.

The rostral is slightly larger than the first supralabial. From above it is visible only as a small triangle. It occupies a slightly longer segment of the labial edge than does the mental. Pairs of medium-sized nasals, very large prefrontals, and smaller frontals form a sequence of enlarged segments along the dorsal surface of the head. The posterior edge of the frontals extends to a level that corresponds to the middle or posterior edge of the third supralabial. The parietal region is covered by irregularly subdivided segments. These are often not rectangular, but are invariably significantly smaller than the frontal.

The angulus oris is often poorly defined. Minor asymmetries in labial size (and hence in labial numbers) are common. There are three supralabials, the second of these somewhat larger than the first and third. The first postsupralabial is very short and approximately the height of the third supralabial. The first, second, and third interlabial sutures run anterodorsally at angles of 20 degrees, 40 degrees, and 50 degrees (and the suture between the third supralabial and the postsupralabial runs at an angle of 30°) to the labial edge. The ocular is more or less quadrangular and is in contact with the second and third supralabials. Dorsally it is in broad contact with the prefrontal and may be in point contact with the frontal. Posteriorly it is followed by the dorsalmost (postocular) segment of the first intercalated dorsal half-annulus, though the next (temporal) segment ventral to this may achieve point, and occasionally wider, contact. The eye is large, clearly apparent, and situated in the anterior half of the ocular.

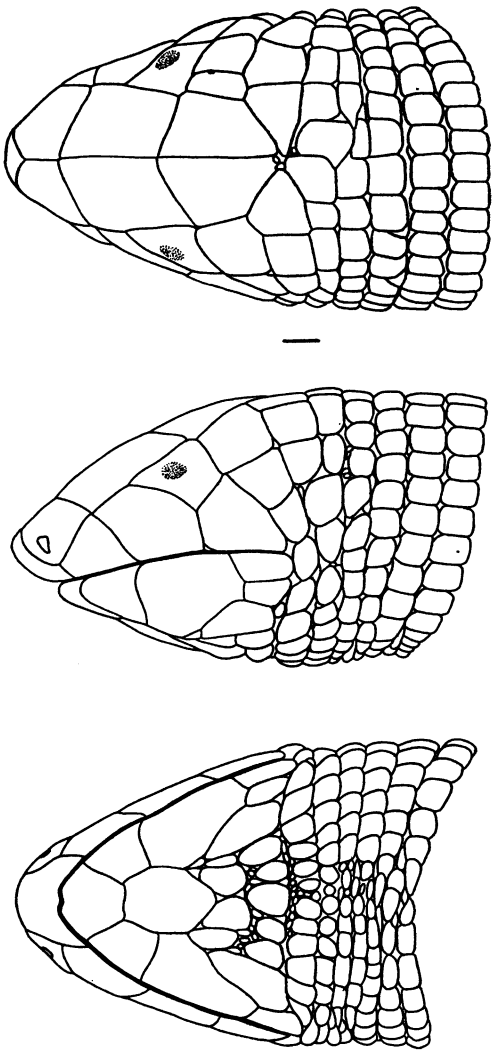


FIG. 29. *Amphisbaena darwini darwini*. Dorsal, lateral, and ventral views of the head of the lectotype, M.H.N.P. No. 3112, from Montevideo, Uruguay. The line equals 1 mm. to scale. Drawn by V. Cummings.

The snout is slightly prognathous, and the shallow lower jaw is inserted within it. Its anterior tip corresponds to the level of the

nostril. The mental is medium-sized and flanked on each side by relatively small first infralabials; its posteriorly convex tip inserts into the anterior aspect of the shield-shaped postmental. The first infralabials are in broad contact with the anterolateral tips of the postmental; the large second infralabials maintain twice as long contact with its sides. The third infralabials are generally twice as long as wide, wider anteriorly, where they are in contact with the malars, than posteriorly, where they often extend caudally slightly beyond the angulus oris. The malars are large and subtriangular; their anteromedial tips are in point contact or excluded from contact with the postmental; in one specimen these tips were divided off by a suture. The postgenial region is confused. There are two to four first postgenials, the lateralmost generally enlarged, anteriorly triangular, and enclosing the posteriorly pointed tip of the postmental between them. Often there is a slightly smaller, azygous segment in medial contact with the posterior tip of the postmental. The three to six, generally five, irregularly shaped segments of the second postgenial row include two wedge-shaped ones that appear to have been divided from the posteromedial edges of the malars. The row curves caudad and may be interrupted on the midline by the medial segment of the first postgenial row. The postmalar row forms a double curve and is composed of eight to 12, generally nine or 10, segments of irregular size. The confusing location of the angulus oris in some cases yields the impression that the postmalar row is absent.

Dorsally the first body annulus sweeps anteriorly. It divides near the level of the angulus oris to produce a first intercalated dorsal half-annulus that includes the temporals and postoculars. The first body annulus continues dorsad to include the (parietal) segments that surround the posterior aspects of the frontals. In a few specimens there is a secondary division into a partial or complete dorsal half-annulus, intercalated between first and second body (in some cases third and fourth) annuli and often fusing with them asymmetrically. The following annuli lose their anterior inclination by the suture posterior to the fourth, which lies in a plane normal to the long axis of the animal. The first eight annuli appear narrowed and separated by markedly wider folding lines that often give them and the one or two posterior ones a shortened and more convexly curved appearance after preservation. Their midventral segments are markedly reduced, and considerable irregularity is common in this region. The remaining annuli lie in planes more or less normal to the long axis of the trunk, though some anterior ones may show some degree of posteriorly concave curvature in dorsal view.

There are 178 to 199 (sample means, 179.5 to 195.2) body annuli from the level of the angulus oris to that including the pore-bearing precloacals. Irregularities in the alignment of annuli are relatively common along the trunk. There are 13 to 18 dorsal and 16.5 to 22 modal numbers of ventral segments to a midbody annulus. The variation here is quite marked, and differences of one to three occur between adjacent annuli. Even large specimens lack diagonal folding lines.

The cloacal region is characterized by two to five (almost invariably four) precloacal pores or pore scars. When fully expressed in mature males, the pore cores have a diameter less than one-sixth (rarely one-fourth) of the length of the pore-bearing segments. The

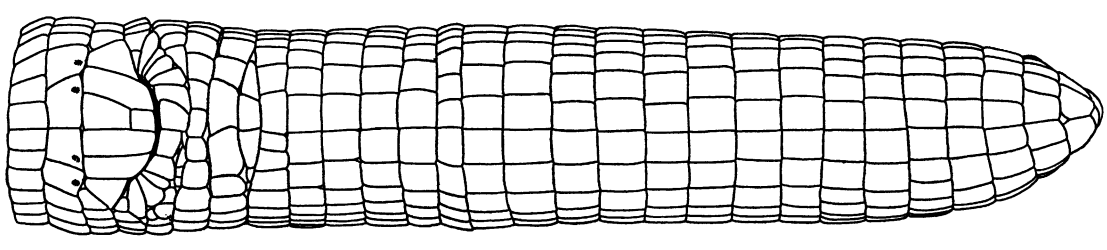


FIG. 30. *Amphisbaena darwini darwini*. Ventral view of cloaca and tail of the lectotype, M.H.N.P. No. 3112, from Montevideo, Uruguay. The line equals 1 mm. to scale. Drawn by V. Cummings.

lateral ones may be smaller than the medial ones, and some pore scars may lack cores. There are six to eight (generally six) more or less subequal segments in the short, segment-shaped precloacal shield. Intersegmental sutures may run in parallel or radiate in a fan-shaped pattern, and the medial or lateral-almost (of the series of six) may be the largest. The postcloacals number nine to 15 (generally 10 to 12), and their median pair is the largest. The cloacal region corresponds to three or four, generally three and rarely and asymmetrically two, lateral annuli. It is followed by six to eight caudal annuli, equivalent in length to the body annuli, which run up to and include the autotomy annulus. Thereafter the remaining annuli of the total series of 18 to 23 caudals become significantly longer. The autotomy annulus is characterized by being narrower and marking a discontinuity in the caudal proportions. One-quarter of the specimens had their tails broken at this point. The ventral surface of the tail is flattened; the section beyond the autotomy level may have a ventral crease. A similar dorsal folding line is shown from the level of the cloaca, up to and slightly beyond the autotomy annulus in slightly shrunken specimens, but is indicated only by intersegmental suture alignment. At its base the tail is wider than high; the part beyond the autotomy annulus is swollen in all dimensions and vertically rather than horizontally oval. The dorsal tip bears a trace of a vertical keel.

The lateral sulci are clearly marked beginning at the level of the twentieth to thirty-fifth body annulus and continuing to that of the cloaca. They are approximately as wide as a bordering segment and filled with irregularly shaped segmental fragments. There is neither a dorsal nor a ventral sulcus, though the midventral intersegmental sutures are aligned.

The middorsal segments are approximately one and one-half times as long as wide; the midventral ones are from one and one-quarter to two times as wide as long. Though considerable proportional variability exists, the medial segments are generally the widest, both dorsally and ventrally.

RANGE: Southern, western, and central portions of Uruguay.

Amphisbaena darwini trachura Cope

Plate 37, figures 2, 3; plate 38, figures 3–6; plate 39, figure 5; plate 40, figures 3–7; text figures 6–12, 31, 32

Amphisbaena mildei PETERS, 1878, p. 780. *Terra typica:* "Porto Alegre," Rio Grande do Sul, Brazil. Holotype: Z.M.U. No. 6255 (possibly lost). *Nomen oblitum.*

Amphisbaena trachura COPE, 1885, p. 189. *Terra typica:* "San Joao do Monte Negro" = Montenegro, Rio Grande do Sul, Brazil. Holotype: A.N.S.P. No. 12988.

DESCRIPTION: This medium-sized form of *Amphisbaena* agrees with the typical race except as indicated. (Since the lead-colored specimens may ultimately require nomenclatorial recognition, their characteristics, if distinct, are indicated in parentheses). The dorsal color is produced by a combination of dark ground color and very marked central pigment emphasis. Both extend ventrally to a level some two to three segments below the lateral sulci, after which the ground color of the segments fades drastically. The darkened dots may shrink or become lighter or do both; they often become reduced to a rectangular rather than rounded, asymmetrically placed zone. The expression of the edge markings appears to be independent of central pigment emphasis; both or either may be emphasized. Many specimens have all segments of the ventral surface pigmented; the segmental pigment dropout is then restricted to the chin and anterior throat regions. Other individuals have a zone of dropout covering much of the ventral surface. The ventral portion of the narrowed autotomy annulus often is emphasized with pigment. (The individual segments appear to be of a uniform dark lead background color, which is sharply emphasized by the edge marking of the anterior sixth. Careful examination shows a significant lightening of a rounded area in the center of each segment. The ground color fades out gradually on the sides of the body, but the edge markings generally continue uninterrupted across the ventral surface. Dropouts are thus restricted to the throat region, to the cloacal shield, and to irregular midventral spots in other specimens. The dorsal surfaces of head and tail are markedly darkened.)

The head appears slightly more robust in these larger specimens, and the neck shorter

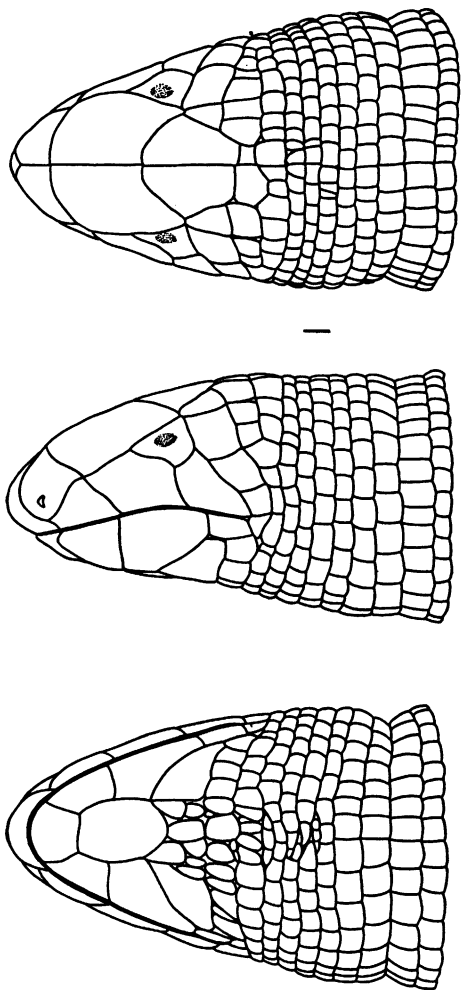


FIG. 31. *Amphisbaena darwini trachura*. Dorsal, lateral, and ventral views of the head of the holotype, A.N.S.P. No. 12988, from Montenegro, Rio Grande do Sul, Brazil. The line equals 1 mm. to scale. Drawn by V. Cummings.

than in the typical form. The posterior edges of the frontal and the parietal region are generally more irregular. The general shortening of the frontals appears in some specimens to have been produced by irregular sutures that completely or partially divide off their posterior tips. This often occurs asymmetrically. In some instances the segment thus formed has completely or partially fused with one of the dorsal segments of the first body annulus, which gives the impression of laterally widened parietals. Such enlargement is usually asymmetrical, and the segment size is in no case more than one-half of that of the frontal. (More than one-half of the specimens show one or two pairs of such enlarged parietals.)

The interlabial sutures run at angles between 45 degrees and 70 degrees, though these show some variation. (The ocular appears to be somewhat larger than that of typical specimens.) The contact distance between the first infralabials and the postmental is approximately equal to that between the latter and the second infralabials. The malars vary widely. They may be in contact with the postmental (more frequent in northern populations) or excluded from it by the lateralmost first postgenials; they are often and asymmetrically subdivided. The postgenial region is confused, and some 15 per cent of the specimens have only a single postgenial row. The first row contains two to five, generally two or three, segments. The second postgenial row contains three to six, generally four or five, segments. The irregular postmalar row contains seven to 13, generally nine to 11, segments.

The first six to eight annuli are narrowed, and the trunk is widest almost immediately posterior to the eighth annulus. Specimens have 168 to 208 (sample means, 176 to 201) body annuli, with irregularities in annular alignment generally restricted to the nuchal and cloacal region. The trunk lacks intercalated half-annuli. There are 14 to 21 dorsal and 17 to 22.5 modal numbers of ventral segments to a midbody annulus.

The cloacal region is characterized by four, rarely by three, precloacal pores, followed by six to eight, generally by six, precloacal, and nine to 14, generally 10 to 12, postcloacal segments. The autotomy level falls on the fifth to eighth (eighth or ninth), generally the sixth or seventh, caudal annuli. There are 15 to 22 (sample means, 17 to 20) caudal annuli.

In typical specimens the tail is markedly swollen both dorsally and laterally after the autotomy constriction. It is relatively short, and the dorsal third to half of the swollen portion has the annuli more deeply incised. In adult specimens the segments of this portion are modified into rounded tubercles. Those of the distalmost annuli have secondary, caudally directed, projecting points. The extreme tip is formed by a pair of tubercles, i.e., the

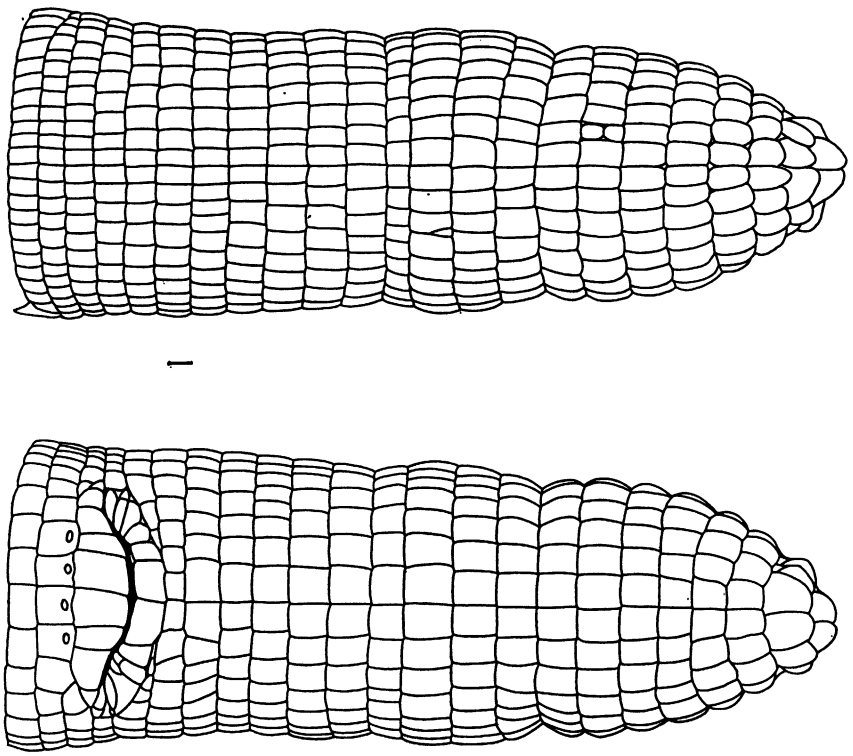


FIG. 32. *Amphisbaena darwini trachura*. Dorsal and ventral views of cloaca and tail of the holotype, A.N.S.P. No. 12988, from Montenegro, Rio Grande do Sul, Brazil. The line equals 1 mm. to scale. Drawn by V. Cummings.

distal annulus has folded upon itself, and there is no irregularly segmented tip. Specimens from coastal Rio Grande do Sul and from the areas of intergradation show various combinations of longer tails, reduced tuberculation emphasis, and reduced number of tuberculated segments. (Those with lead pattern have tails reminiscent of those of the typical race.)

Some 30 per cent of the specimens have some splitting of middorsal portions of the annuli in the cloacal and caudal regions. The existence of this in juveniles suggests that it represents a fixed pattern.

RANGE: Brazil (São Paulo to Rio Grande do Sul) into northern Uruguay and extreme northeastern Argentina.

Amphisbaena darwini heterozonata Burmeister

Plate 37, figure 4; plate 39, figures 1–4; plate 40, figure 8; text figures 6–12, 33, 34

Amphisbaena heterozonata BURMEISTER 1861. vol. 2, p. 527 (*Lepidosternon heterozonatum* Burmeister, 1861, vol. 1, p. 309, in error). *Terra typica:* "Bei Mendoza und Tucuman"; restricted to "Mendoza," Argentina (Lorenz Müller, 1941, p. 195); herein corrected to Tucumán, Argentina. Types: Originally in the Zoological Institute in Halle (Lorenz Müller, 1941); lost.

DESCRIPTION: This medium to small-sized form of *Amphisbaena* agrees with the typical race except as indicated. As in *A. d. trachura*, the dorsal coloration is produced by a combination of background color and central pigment emphasis. Variable fractions of each population have the dotting restricted to the anterior portion of the trunk; it fades out near midbody, leaving the segments evenly colored. The dorsal surfaces of head and tail are very dark. The sides of the tail bear the halfmoon of dotted segments. Relatively few of these specimens show strong edge marking that invades or crosses the ventral surface. The dots often are markedly noticeable to the

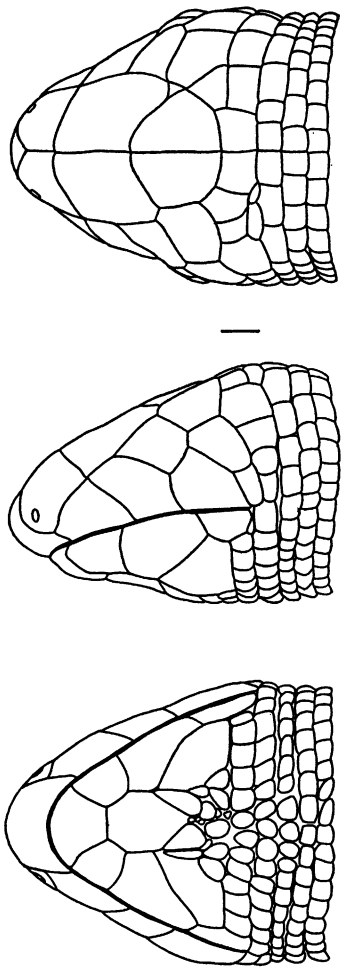


FIG. 33. *Amphisbaena darwini heterozonata.* Dorsal, lateral, and ventral views of M.S.N.G. No. CE28313E from La Plata, Buenos Aires, Argentina. The line equals 1 mm. to scale. Drawn by V. Cummings.

fourth or fifth segment row below the lateral sulcus. The ventral surface is ordinarily nonpigmented from throat to cloacal shield. Many specimens have the ventral surface of the tail pigmented, and the autotomy annulus is generally marked.

The head appears very short, and the angle between the sides of the head seems to be more obtuse than that of the other two races. The neck is shortest, and the trunk very rapidly achieves full diameter. These differences in head proportions between the races cannot be attributed to allometric growth; they hold true for juveniles as well.

The frontals are short, and their posterior edge is often irregularly scalloped. The parietal region is again extremely irregular; enlargement of these segments is rare. The interlabial sutures run at angles between 45 degrees and 75 degrees, though these show some variation.

The postmental gives the impression of being somewhat smaller than that of the other forms. Contact between it and the first infralabial is generally shorter than that between it and the second. The malars are rarely subdivided, but there is no pattern to the contact of their anterior tips with the postmental; this may be broad, point, or absent. There is some confusion in the postgenial region. The first postgenial row contains two to four, almost invariably two, large segments that enclose the posterior tip of the postmental between them. The third postgenial, when present, is smaller and projects between the large ones. Fewer than 5 per cent of the sample lacks a second row. The second postgenial row contains two to seven, generally three, four, or five, smaller segments. The postmalar row contains six to 16, generally nine, 10, or 11, segments, with the values slightly lower in the western part of the range.

The majority of specimens have only a single intercalated dorsal half-annulus anterior to the first body annulus. The sutures defining the second body annulus lie in planes normal to the long axis of the trunk. The first six annuli are narrowed; a variable number may show a posteriorly concave curvature in dorsal view. The trunk achieves its full width by the fourth to sixth postcephalic annulus. Specimens have 190 to 207 (sample means, 191 to 203) body annuli, with irregularities in alignment generally restricted to nuchal and cloacal regions. The trunk lacks intercalated half-annuli. There are 14 to 18.5 dorsal and 17.5 to 22 modal numbers of ventral segments to a midbody annulus.

The cloacal region is characterized by four, rarely by two to six, precloacal pores. The segments bearing these are followed by five to eight, generally (almost exclusively in the western region) by six, precloacal, and by eight to 16, generally by 10 to 13, postcloacal segments. The autotomy level falls on the fifth to eighth, generally on the sixth or

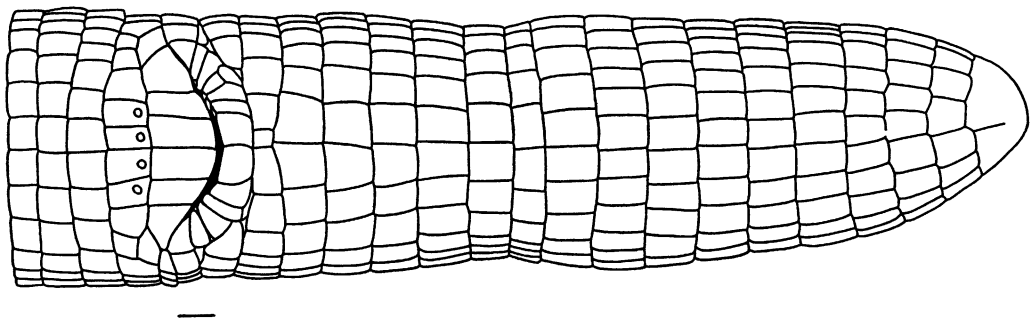


FIG. 34. *Amphisbaena darwini heterozonata*. Ventral view of cloaca and tail of M.S.N.G. No. CE28313E from La Plata, Buenos Aires, Argentina. The line equals 1 mm. to scale. Drawn by V. Cummings.

seventh, caudal annulus. There are 13 to 17 (sample means, 14 to 16.2) caudal annuli.

The tail is relatively short; it swells noticeably after the autotomy constriction which falls near the middle of its length. The distal portion is wider than high; terminally there is a vertical fold. The interannular sutures are sharply marked up to the distal tip, and their segments are clearly defined. Although the segments of the dorsal tip may appear faintly swollen in samples from the northeastern portion of the range, in no instance are they tuberculate.

RANGE: Argentina (Tucumán to Buenos Aires) north into southern Bolivia and central Paraguay.

LOCALITY RECORDS: ARGENTINA: — (Boettger, 1893; Burt and Burt, 1930; Parker, 1928); M.A.C.N. Nos. 7227a, 7227b, 17869; M.C.S.N. Nos. a, b; M.H.N.P. Nos. 08.94a, 08.94b; N.H.M.B. No. 66a; N.M.B. No. 4267; N.M.W. No. 8158:1; S.M.F. Nos. 11804–11807; U.S.N.M. No. 73513. *Buenos Aires:* — (Birabén, 1954); K.M. Nos. R4426, R4427, R4429–R4431; M.A.C.N. Nos. 2716, 2717; M.G. Nos. 983:60, 983:61; M.S.N.G. No. CE36600; N.M.B. No. 3805; P.U.M. No. 398; S.M.F. Nos. 11809, 11810, 55133, 56604; U.M.M.Z. No. 94086. Isla Martin Garcia: I.N.M. No. 51 (intermediate with *d. darwini*); M.A.C.N. No. 6572. San Pedro: M.A.C.N. Nos. 4505, 7911. Rojas: C.G. No. 2535; M.A.C.N. No. 15225. La Luisa: M.A.C.N. No. 16127. Gonzales Catán: L.I.H.U.B.A. Nos. 244, 249. Zelaya: M.A.C.N. Nos. 6640, 6875, 7214, 17841, 17842. Pilar: M.A.C.N. No. 4616. San Isidro: M.A.C.N. No. 2689. Bella Vista (30 kilometers northeast of Buenos Aires): C.G. No. 2536. Moreno: M.A.C.N. No. 8936. Buenos Aires (Capital Federal): C.G. Nos. 1341, 1343, 2800; M.A.C.N. Nos. 3150, 3669, 3686, 4084, 6124, 6125, 6426, 6571, 6903, 7166, 7613a, 7613b, 7910, 9512, 11958, 17827–17829, 17836–17838, 17847, 17849, 17851, 17854, 17862–17864, 17866–17868, 17870–17874. Vincente Lopez (Capital Federal): L.I.H.U.B.A. No. 614; M.A.C.N. No. 6259. Flores (Capital Federal): L.I.H.U.B.A. Nos. 248, 1066. Barrio de Villa Devoto (Capital Federal): C.G. No. 2534. Ezpeleta: L.I.H.U.B.A. Nos. 914, 1496. City Bell: J.A.P. No. 4316. Castelar (25 kilometers southeast of Buenos Aires): M.A.C.N. No. 9676. Punta Lara: M.A.C.N. No. 6276. La Plata: (Burt and Burt, 1930); C.N.H.M. Nos. 12362, 12363; K.M. Nos. R4424 (this is *d. darwini*, and the locality seems erroneous), R4433; M.S.N.G. Nos. CE9552, CE28313a–28313h, CE-36601A.a.–CE36601A.h, CE36601B.1, CE36601B.2, CE36601D; R.M.N.H. No. 4838; U.S.N.M. No. 22763. Gandara: M.A.C.N. No. 5938. Chacosmús: M.A.C.N. No. 16632. Ajo: N.M.W. No. 8158:2. Maipú: M.S.N.G. Nos. CE28314a, CE28314b. Iraola, Parque Perevra: L.I.H.U.B.A. No. 247. Tandil ("Sierra cerca de la ciudad"): C.G. No. 2533; M.A.C.N. Nos. 11355, 11771. Sierra Bajas: (Nágera, 1915); M.A.C.N. No. 4495. Pirovano: C.G. No. 2532; M.A.C.N. Nos. 10179–10183. Sierra de la Ventana: (Koslowsky, 1895); M.A.C.N. No. 17883. Bahia Blanca: M.S.N.G. No. CE28315; N.M.B. No. 4268. ?Ramos Mejía: M.A.C.N. No. 6820. *San Luis:* — I.B.M. No. 0221-R. *Cordoba:* Achiras: A.M.N.H. No. 65191. Río Tercero, Estancia "La Pastora": (Hellmich, 1960); Z.S.M. No. 227/1933. Alta Gracia: I.M.L. No. 0013. Tanti, Dept. Punilla: M.A.C.N. No. 10249. Valle Hermoso: L.I.H.U.B.A. Nos. 242A, 242B, 243A–243E; M.C.Z. Nos. 67020, 67021. *Santa Fé:* — Z.S.M. No. III. Santa Fé: M.A.C.N. No. 7244. Near Santa Fé: C.M. No. 2613. Estancia La Germania: Z.S.M. No. I (seven specimens). Galvez: (Hellmich, 1960); Z.S.M. No. 225/33. *Entre Rios:* — H.M. No. 2049. ?Gualeguychú:

(Freiberg, 1939). Villa Urquiza, near Paraná: M.S.N.G. No. CE36601C. *Misiones:* — M.A.C.N Nos. 3761–3763. *Chaco:* — M.A.C.N. Nos. 4167, 17844. Resistencia: (Peracca, 1895); I.M.Z.U.T. Nos. 968A, 968B; M.A.C.N. No. 7051. *Tucumán:* — (Burmeister, 1861; Lorenz Müller, 1941; Peracca, 1895; Strauch, 1881); I.M.L. Nos. 29, 58A–58C; I.M.Z.U.T. Nos. 967B, 967C; M.A.C.N. Nos. 17852, 17865, 17835, 17890, 17846, 17861, 3831; N.M.W. No. 12334. Concepción: K.M. No. R4435. Kilometer 7, Villa Marces Paz, Tafí: L.I.H.U.B.A. No. 245. Serra de San Javier, Tafí: L.I.H.U.B.A. No. 246. Tafí Road, south of Tucumán: M.C.Z. No. 12360. Capital: C.G. Nos. 3312–3317; I.M.L. Nos. 249A, 249B, 282A, 282B, 303A, 303B (one unnumbered); M.C.Z. No. 84334. *Catamarca:* — M.A.C.N. No. 3320. *Salta:* — (Peracca, 1895); C.A.S. Nos. 84772, 84773; I.M.Z.U.T. No. 960; M.A.C.N. No. 17826; Z.M.U. Nos. 26312A–26312C. Rosario de la Frontera: I.M.L. No. 0088. *Jujuy:* El Volcán: M.A.C.N. Nos. 6973, 6974.

BOLIVIA: Caixa: (Peracca, 1897); I.M.Z.U.T. No. 1958. Río Pilcomayo: Z.M.U. No. 26416.

PARAGUAY: — M.A.C.N. Nos. 17848, 17850. Guajho, Casaso San Pedro: M.A.C.N. No. 8211. Chaco: B.M. No. 1901.3.9.1.

URUGUAY: — (Burt and Burt, 1930; Fritz Müller, 1885); A.M.N.H. No. 42967; (B.M. No. 89.12.16.30, "West Indies"); M.C.Z. Nos. 10118, 12317; N.M.B. No. 4269; U.S.N.M. No. 70476; Z.M.U. 6.1936/19. *Soriano:* Soriano: C.M. Nos. 38961–38963. Estancia "Santa Rita": Z.V.C. R245. *Colonia:* Carmelo: M.A.C.N. No. 2711. Nuevo Palmira: M.N.H.M. No. 180. *San José:* Sierra de Mahoma: Z.V.C. No. R475. Rincon del Pino: (Burt and Burt, 1930); U.S.N.M. Nos. 65526, 65527. *Montevideo* (all sites lie in the immediate vicinity of the city): — (Devincenzi, 1925; Duméril, 1851; Duméril and Bibron, 1839; Hellmich, 1960); B.Y.U. No. 16131; I.M.Z.U.T. No. 1316; K.M. Nos. R4425, R4432; M.N.H.M. Nos. 208, 214, 316, 581, 781, 895, 897; M.H.N.P. Nos. 569, 3102, 3107, 3112 (types of *darwini*), 3113; M.S.N.G. Nos. CE28309a–28309c; N.M.W. Nos. 12338:1–12338:9; U.S.N.M. Nos. 68033, 73535; Z.M.U. Nos. 1380a, 1380b; Z.S.M. No. 224/33; Z.V.C. No. R.36. Cerro: K.M. No. R4428. Colón: C.G. No. 2208. Malvín: M.N.H.M. Nos. 900A, 900B. Prado: M.N.H.M. No. 179. La Unión: Z.V.C. No. R311. Carrasco: (Devincenzi, 1925); C.G. No. 2037; M.N.H.M. Nos. 212, 585, 766, 778. Camino Maldonado: Z.V.C. No. R127. Punta Carretas: M.N.H.M. Nos. 901A–901C. Estación Llamas: M.N.H.M. No. 576. Sayago: M.N.H.M. No. 896; Z.V.C. No. R300. "Cho." Cuchilla, Pereira: Z.V.C. No. R135. Paso de la Arena: M.N.H.M. Nos. 205, 211. *Canelones:* Empalme Sauce: M.N.H.M. No. 894. Balneario Solis: M.N.H.M. No. 904. *Lavalleja:* Route 12, kilometer 10: M.N.H.M. Nos. 898A, 898B. *Maldonado:* — (Burt and Burt, 1930); A.N.S.P. Nos. 9688, 9689; M.C.Z. No. 3021; U.S.N.M. No. 65529. Sierra de Animas: Z.V.C. No. R440. Isla de Lobos: Z.V.C. Nos. R105.1–105.2. *Rocha:* Rocha: B.Y.U. Nos. 16125, 16126, 16128–16130; M.N.H.M. No. 177. St. Vicente de Castillos, 15 kilometers north of: C.N.H.M. No. 10324. *Durazno:* — (Burt and Burt, 1930); U.S.N.M. No. 65539. *Treinta y Tres:* Santa Clara de Olimar: Z.V.C. Nos. R259.1, R259.2. *Cerro Largo:* — (Burt and Burt, 1930); U.S.N.M. No. 65612. *Rio Negro:* Sarandí de Navarro: M.N.H.M. No. 860. *Tacuarembó:* Paso Manuel Díaz: M.N.H.M. No. 905. Tambores: M.N.H.M. Nos. 206, 207. *Rivera:* Park Gran Britania: B.Y.U. Nos. 11477, 11478, 11480–11482; K.U. No. 31678. Estancia Agraria: M.N.H.M. Nos. 899A–899E. *Artigas:*— M.N.H.M. No. 172. "Proximo al pueblo Bernabe Rivera": Z.V.C. No. R262. Los Catalanes: Z.V.C. No. R228.

BRAZIL: — H.M. No. 4677; M.S.N.G. unnumbered; N.H.M.B. No. 66b; N.M.W. Nos. 29a–29c (Anhao), 12335:5–12335:7; R.M.N.H. No. 3563; U.R.G.S. Nos. 0678, 0744, 1013, 1014; Z.M.U. Nos. 1382, 1383. Rio Grande do Sul: — (Boettger, 1893); B.M. No. 91.3.16.3; K.M. Nos. R441, R442, R4434; S.M.F. Nos. 11802, 11803; U.R.G.S. Nos. 626, 630. Santana (=Livramento): B.Y.U. Nos. 11484–11486. Pelotas: M.R.C.N. Nos. 1676, 1677, 1933, 1934. Restinga Seca: D.Z. No. 6534. Santa Maria: C.G. No. 1065; M.R.C.N. Nos. 2294, 2295; U.R.G.S. Nos. 1003, 1005. Cachoeira do Sul: U.R.G.S. Nos. 1008, 1009. Candelária: M.R.C.N. No. 1489. Santa Cruz do Sul: N.M.W. No. 12336:1. Tabatinga (or Garcia Ferraz, specimen labeled only Garcia): H.M. No. 309. Barro do Ribeiro: D.Z. No. 3251. São João do Monte Negro (=Montenegro): (Cope, 1885); A.N.S.P. No. 12988 (holotype of *trachura*). Passo Fundo: M.R.C.N. No. 966. Faroupilha: M.R.C.N. No. 787. Viamão: M.R.C.N. Nos. 1014, 1020, 1064–1066, 1141–1143, 1162, 1420, 1422, 1437, 1537; U.R.G.S. Nos. 1006, 1007, 1010. Pôrto Alegre: H.U.J. Nos. 5949, 5950; M.R.C.N. Nos. 1231, 1446, 1776, 2008, 2066, 2067; U.R.G.S. Nos. 627, 1004; Z.S.M. Nos. 661/0, 663/0. Canoas: C.G. Nos. 1062, 1064; M.R.C.N. No. 2279; U.R.G.S. No. 1002. São Leopoldo: M.R.C.N. Nos. 1938, 2105–2110. São Francisco de Paula: M.R.C.N. Nos. 1432, 2042–2045. Cidreira: D. Z. No. 3253. Osório: C.N.H.M. No. 80101; M.R.C. N. No. 2065; U.R.G.S. Nos. 554, 629. Emboaba, Tramandaí: C.A.S. No. 94167; C.G. Nos. 2835–2838; 3151–3154. Tôrres: M.R.C.N. No. 2013;

U.R.G.S. No. 632. *Santa Catarina:* — B.M. No. 88.2.7.7.2.; N.M.W. Nos. 12339:1–12339:4. Lagoa: D.Z. Nos. 1920, 6388, 6671. Boiteuxburgo: H.M. No. 5040. Bugre: D.Z. No. 6517. Tres Barras: D.Z. No. 6642. Joinville: N.M.W. Nos. 12337:1–12337:5. *Paraná:* ?Balsa Nova: D.Z. No. 6659. ?Novo Capivari: D.Z. No. 6533. Paulo Freitas: D.Z. Nos. 6538, 6651. Rio Azul: D.Z. No. 6645. Texeira Soares: D.Z. Nos. 1895, 6665. Palmeira: D.Z. No. 6895. Rio Negro: H.M. No. 2869. Tijuca Preto, near Rio Negro: H.M. Nos. 2865A–2865D, 2865F–2865N. Lapa: D.Z. No. 6060. Engenheiro Blei: U.M.M.Z. No. 103074. Serrinha: D.Z. No. 6543. Roca Nova: D.Z. No. 6541. Paranagua: H.M. Nos. 3978A, 3978B. Carambeí: D.Z. No. 6441. Castro: D.Z. Nos. 1280, 6516, 6539, 6656, 6894. Piraí: D.Z. Nos. 6535, 6536. *São Paulo:* São Paulo (including Ypiranga, Instituto Butantan): (Ihering, 1898); D.Z. No. 279; H.M. No. 1879. São Manuel: D.Z. No. 6655. Aurora: D.Z. No. 6542. Santo Anastacio: D.Z. No. 6553. *Mato Grosso:*—S.M.F. No. 11811.

Amphisbaena munoai Klappenbach

Plate 41; plate 42, figure 7; text figures 18–28, 35–37

Amphisbaena muñoai KLAPPENBACH, 1960, p. 3. *Terra typica:* "Cerro de Animas, Departamento de Maldonado," Uruguay. Holotype: M.N.H.M. No. 587. Paratypes: M.N.H.M. Nos. 173A–173D, 181A–181F, 583A–583E, 586, 588–591, 718A, 718B, 862A–862C, 863, 865A–865C (Cerro de Animas); M.N.H.M. Nos. 178A, 178B, 182 (Cerro San Antonio, Piriapolis, Maldonado); M.N.H.M. No. 714 (Carpintería, Rivera); M.N.H.M. No. 716 (Aguas Blancas, Lavalleja); M.N.H.M. Nos. 861A, 861B (Zapicán, Lavalleja); Z.V.C.-R. No. 37-1 (Cerro de Arequita, Lavalleja); M.N.H.M. No. 864 (Sierras de Aceguá, Cerro Largo); Z.V.C.-R. Nos. 38, 142 (Cerro, Montevideo).

DIAGNOSIS: A relatively small form of *Amphisbaena* without major fusions of head shields, with the prefrontals by far the largest segments on the dorsal surface of the head and the medium-sized postmental the largest segment on the ventral surface, with a strongly bent rostral edge, a relatively short head, and enlargement of segments in the postocular and parietal regions. The form has 196 to 219 body annuli, 16 to 21 caudal annuli, a clearly marked autotomy site that falls on the eighth to ninth postcloacal annulus, 12 to 14 dorsal and 13 to 20 ventral segments to a midbody annulus, and four large, clearly marked, round, precloacal pores in males, and only pore scars in females. The tip of the tail lies below the caudal center line. Only the lateral sulci are noticeable. Specimens are brown dorsally, lighter ventrally. The dorsal segments are evenly pigmented, the raphes are much lighter, the pigment density fades below the lateral sulcus, and the pigmentation drops out by segments, four to six segments below the lateral sulcus. Some specimens (northern end of range) show marked edge marking on the sides of the trunk; other specimens may show some dotting of the lightened segments.

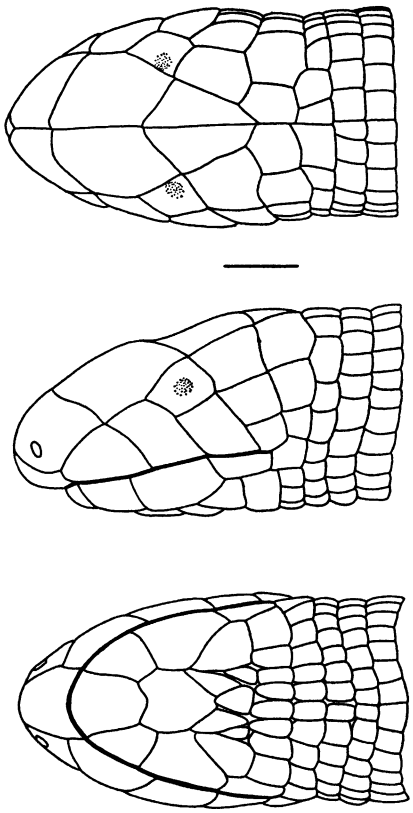


FIG. 35. *Amphisbaena munoai.* Dorsal, lateral, and ventral views of the head of C.G. No. 1815 from Cerro de Animas, Departamento Maldonado, Uruguay. The line equals 1 mm. to scale. Drawn by V. Cummings.

DESCRIPTION: This small-sized species of *Amphisbaena* is medium brownish dorsally and light in color ventrally. The dorsal segments are more or less evenly pigmented. Some show irregular zones of darker pigmentation, and all intersegmental and interannu-

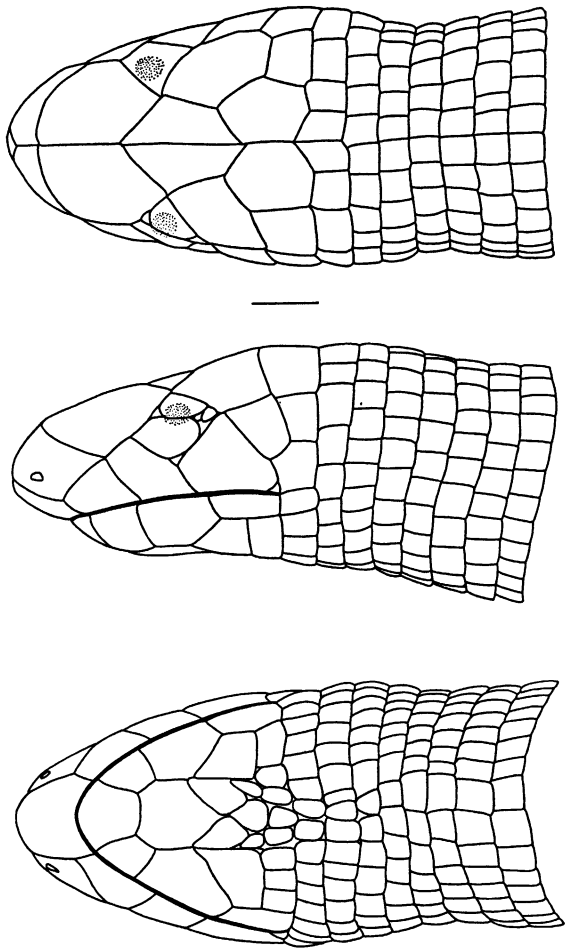


FIG. 36. *Amphisbaena munoai.* Dorsal, lateral, and ventral views of the head of M.R.C.N. No. 1182 from Viamão, Rio Grande do Sul, Brazil. The line equals 1 mm. to scale. The split ocular represents a unilateral anomaly. Drawn by V. Cummings.

lar raphes are light. The pigmentation becomes both lightened and mottled below the lateral sulci, and the dark pigment drops out by segments some four to six segments below the sulci. The head shields are but slightly darker; the rostral tip and the lower jaw are light-colored, as is the entire ventral surface. The subcaudal zone may be clear or may have some or all segments pigmented; in the latter case, there may be some pigment emphasis of the autotomy annulus.

The head segmentation is characterized by a lack of major fusions, by the very large prefrontal, and by the enlargement of segments in the postocular and parietal regions. The entire snout is high, and the zone covered by the nasal and prefrontal segments remains relatively high and curves down sharply only near the rostral tip. The head is otherwise wider than high. The rostral region does not project markedly beyond the fairly shallow lower jaw. The posterior portion of the head is of approximately the same diameter as the trunk, which is but slightly wider than high.

The tip of the rostral is just visible in dorsal view. Its ventral exposure is equal to or greater than that of the mental. Pairs of large nasals, twice as large prefrontals, smaller frontals, and variably sized and shaped (but invariably enlarged) first parietals follow in sequence along the midline of the head. The second parietals are generally enlarged but normally are not much longer than the segments of the following body annuli. The posterior edge of the frontals corresponds approximately to the level of the angulus oris. There are three supralabials, but a fourth small (postsupralabial) segment in line occasionally appears to lie on the labial edge. The relative size of the supralabials varies, but the second is invariably the smallest, and the interlabial sutures are directed anterodorsally at an angle of approximately 50 degrees. The quadrangular rostral lies in ventral contact with the second and third supralabials, in dorsal contact with the prefrontal, and in posterior contact with the postocular. The frontals and the (temporal) segment below the postocular may attain point contact.

The mental is about the size of the postmental. Its anterior wings occupy a distance of the labial edge equal to that occupied by the rostral. The anterior edge of the postmental is concavely scalloped for the mental insertion, its sides are generally in wider contact with the medium-sized first, than with the much wider second, infralabial, and its bluntly pointed posterior edge is included between two large, teardrop-shaped, first postgenials. The medium-sized, wider than long malars are in contact with the second and the narrow third infralabials; they generally lack contact with the postmental. The median shield of the postgenial region may be very large. Its anterior tip often touches the postmental (and is then counted in the first row); it may even extend the full length of the first

and second postgenial rows. The other segments of the second row are very small. They may form a complete row, or may interdigitate between the posterior corners of the elements of the first row, or, again, be altogether lacking. The frequency of the second and third conditions varies from 20 per cent in the south to 50 per cent in the north. The lateralmost of the seven to 10 segments of the postmalar row are often widened. The postgular region is covered with regular segments.

Dorsally the first body annulus divides to form a single intercalated half-annulus, and its enlarged segments form the shields of the temporal, postocular, and parietal region. The posterior edge of the first body annulus tends to fall in a plane normal to the long axis of the trunk. The third to eighth body annuli tend to be narrowed; the more posterior annuli are of uniform length and lie more or less normal to the long axis of the trunk.

There are 196 to 219 (203 to 219 in Uruguay, 196 to 210 in Rio Grande do Sul) body annuli from the back edge of the third infralabial up to and including the pore-bearing precloacal row. Intercalated dorsal half-annuli are lacking; rarely is there an annular irregularity. A midbody annulus has median counts of 11.5 to 14 dorsal and 13 to 20 (16 to 20 in Uruguay, 13 to 18.5 in Rio Grande do Sul) ventral segments. There is some segmental irregularity, concentrated mainly in the middorsal and the lateroventral regions.

The cloacal region is characterized by four large, round, evenly spaced, precloacal pores in males, and only pore scars in females. The precloacal shield is relatively short and segment-shaped; it is formed of six, rarely seven, large segments. The postcloacal edge is formed of nine to 14 segments, of which the central pair is markedly widened. The lateral rows number two to four.

The tail is cylindrical, with a tendency to be wider than high before, and higher than wide beyond, the narrowed and constricted autotomy annulus which falls on the eighth to ninth postcloacal annuli. There are 16 to 21 caudal annuli up to the partially segmented terminal cap; the last three interannular sutures are generally less deeply inscribed. The distal tip of the tail lies below the caudal midline.

The lateral sulci are clearly marked after about the twentieth body annulus. At midbody, where both of them lie in the top half of the animal, their width is equal to or less than that of one of the bordering segments. There are neither dorsal nor ventral sulci.

At midbody the dorsal segments are one and one-half to twice as long as wide; the midventral segments are approximately one and one-quarter to one and one-half as wide as long.

RANGE: South and central Uruguay to northeastern Rio Grande do Sul.

LOCALITY RECORDS: URUGUAY: (Records marked with an asterisk were cited by Klappenbach, 1960). *Florida:* Isla Mala (under rocks at kilometer 95): B.Y.U. Nos. 16139–16147. *Montevideo:* *Montevideo: M.H.N.P. Nos. A3101A–A3101F. *Cerro: Z.V.C.-R. Nos. 38, 142. *Maldonado:* *Piriapolis, Cerro San Antonio: M.N.H.M. Nos. 178A, 178B, 182. *Cerro de Animas: C.G. Nos. 587, 1619, 1620, 1815, 2038, 2190–2207, 2768, 2769, 2365; M.N.H.M. Nos. 173A–173D, 181A–181F, 583A–583E, 586, 588–591, 718A, 718B, 862A–862C, 863, 865A–865C. *Rocha:* Rocha, 121 kilometers from, in hills: B.Y.U. Nos. 16132–16135. Rocha, pasture near: B.Y.U. Nos. 16137, 16138. **Lavalleja:* Aguas Blancas: M.N.H.M. unnumbered. *Cerro Arequita: Z.V.C. No. R37-1. *Zapican: M.H.N.M. Nos. 861A, 861B. *Cerro Largo:* *Serra de Aceguá: M.H.N.M. No. 864. *Rivera:* *Carpintería: M.N.H.M. No. 714.

BRAZIL: — U.R.G.S. No. 1212; Z.M.U. No.

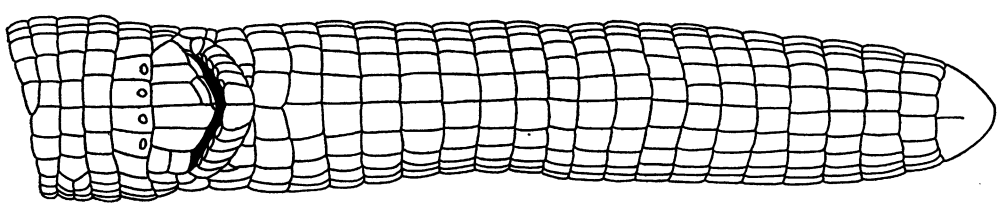


FIG. 37. *Amphisbaena munoai.* Ventral view of cloaca and tail of C.G. No. 1815 from Cerro de Animas, Departamento Maldonado, Uruguay. The line equals 1 mm. to scale. Drawn by V. Cummings.

16828C. *Rio Grande do Sul:* — M.R.C.N. No. 2246 (possibly Z.M.U. No. 6828C). Santa Maria: M.C.Z. Nos. 43297–43299. São Jeronimo: M.R.C.N. No. 2250. Passo Fundo: M.R.C.N. Nos. 967, 968, Viamão: M.R.C.N. Nos. 1144, 1177, 1178, 1182, 1421; U.R.G.S. No. 1011. Pôrto Alegre: M.R.C.N. Nos. 1908, 1930, 1947–1949.

Amphisbaena prunicolor prunicolor (Cope)

Plate 42, figures 1–3; text figures 18–28, 38, 39

Aporarchus prunicolor COPE, 1885, p. 189. *Terra typica:* "Sao Joao do Monte Negro, Rio Grande do Sul, Brazil." Holotype: A.N.S.P. No. 12969.

DIAGNOSIS: This is a medium- to small-sized form of *Amphisbaena*, without major fusions of head shields, with the prefrontals by far the largest segments on the dorsal surface of the head and the medium-sized postmental the largest segments on the ventral surface, with a strongly bent rostral edge, a relatively short head, and generally with enlargement of the segments of the postocular and parietal regions. The form has 180 to 206 body annuli, 18 to 24 caudal annuli, a clearly marked autotomy site that falls on the sixth to ninth postcloacal annulus, 10 to 16 dorsal and 14 to 19 ventral segments to a midbody annulus, and four large, clearly marked, round, precloacal pores in the males, and only pore scars in the females. The tip of the tail tends to lie on or above the caudal center line. Only the lateral sulci are marked, but the dorsal sulcus is often fringed by a row of narrow, elongate segments. Specimens are brown dorsally and generally not or only slightly countershaded. The pigment drops out by segments in a checkerboard pattern in a zone of variable size on the ventral surface. Segments show some central pigment emphasis (particularly in central Rio Grande do Sul).

DESCRIPTION: This medium- to small-sized species of *Amphisbaena* has a dark brownish, often not countershaded, coloration. The dorsal segments are completely pigmented, but the central region of each segment bears a poorly defined zone of denser pigmentation. These areas of central pigment emphasis become more marked below the lateral sulci, where the over-all pigment density may or may not decrease. (The decrease is most clearly marked in the Santa Cruz material in which countershading is induced in this manner, though the pigment dropout does not occur until a much more ventral position.) The most characteristic aspect of the pigmentation is the pigment dropout which gives a checkerboard appearance of alternate light and dark segments. Even the most heavily pigmented specimens show some of this in the gular region, although others show just the cloacals lightened, or a light midventral zone along their entire length. The intersegmental and interannular sutures are lighter

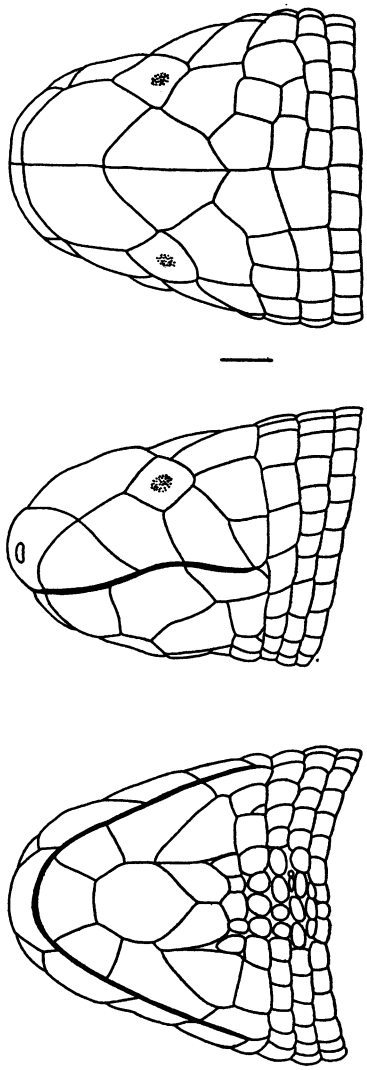


FIG. 38. *Amphisbaena prunicolor prunicolor.* Dorsal, lateral, and ventral views of the head of the holotype, A.N.S.P. No. 12969, from Montenegro, Rio Grande do Sul, Brazil. The line equals 1 mm. to scale. Drawn by V. Cummings.

colored and fade more rapidly in preservatives.

The head segmentation is characterized by a lack of major fusions, by the very large prefrontal, and the enlargement of the segments in the postocular and parietal regions. The snout is relatively high and the prefrontals and nasals cover a more or less swollen surface (see Geographic Variation) that does not curve downward until the very tip. The middle of the frontals marks the site of a maximal reverse curvature; the temporal muscle bulges swell from there and often make the head squarish or higher than wide in cross section. The rostral region projects only slightly beyond the fairly shallow lower jaw. The posterior portion of the head is of a slightly lesser diameter than the trunk; the nuchal region shows some narrowing in certain specimens. The trunk is generally slightly wider than high.

The tip of the rostral is barely visible in dorsal view. Its ventral exposure is approximately equal to that of the mental. Pairs of medium-sized nasals, very large prefrontals, smaller frontals, and of generally large parietals follow in sequence along the midline of the head. The parietal region is often the site of irregularities. For instance, most of the Santa Cruz (Rio Grande do Sul) specimens had showed major and generally asymmetrical divisions of the parietals. The posterior edge of the frontals corresponds approximately to the middle of the third supralabials. There are generally three supralabials, but irregularities are common near the angulus oris. The second supralabial tends to be the largest, and the intrasupralabial sutures are curvilinear and directed generally at angles of 70 degrees, whereas the rostrodorsad angle of the posterior edge of the third supralabial ascends smoothly at an angle of nearly 45 degrees. The quadrangular ocular broadly touches the second and third supralabials, the prefrontals, and the postocular; it is in point contact with the frontal and the (temporal) segment ventral to the postocular.

The mental is smaller than the elongate, shield-shaped postmental. Its anterior wings occupy approximately the same distance along the labial edge as does the rostral. The mental-postmental contact is along a straight line; that between the postmental and the medium-sized first infralabial is much shorter than that with the large second infralabial. The tips of the large malars normally are at least in point contact with the postmental. A pair of large, first postgenials encloses the obtuse posterior angle of the postmental; rarely is there a median third element in this row. The three to six segments of the second row are much smaller; they are missing from some specimens. A row of six to 10 postmalar segments lies between the posterior tips of the narrow third infralabials. The postgular region is only slightly diversified.

Dorsally the first body annulus divides once or twice to provide a single or a double intercalated half-annulus, and to form the various enlarged segments of the postocular and parietal regions. The anterior edge of the second body annulus tends to fall in a plane normal to the long axis of the trunk. The third to seventh annuli are slightly narrowed; the more posterior annuli are of uniform length and lie more or less normal to the long axis of the trunk.

There are 180 to 206 body annuli from the back edge of the third infralabial up to and including the pore-bearing precloacal row. Intercalated dorsal half-annuli are rare, as are

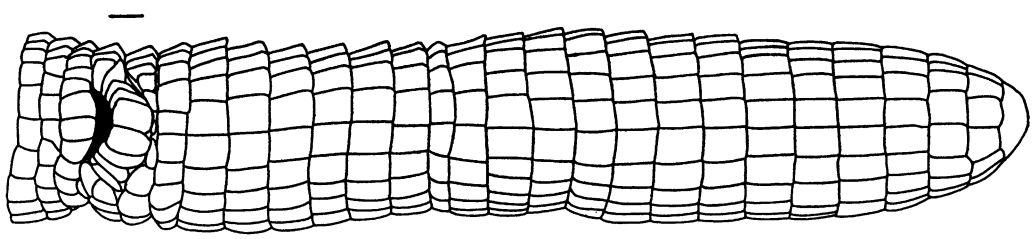


FIG. 39. *Amphisbaena prunicolor prunicolor*. Ventral view of cloaca and tail of the holotype, A.N.S.P. No. 12969, from Montenegro, Rio Grande do Sul, Brazil. The line equals 1 mm. to scale. Drawn by V. Cummings.

annular irregularities. A midbody annulus has a median count of 10 to 16 dorsal and 14 to 19 ventral segments. There is some segment irregularity.

The cloacal region is characterized by four large, round, evenly spaced, precloacal pores in males, and only faint pore scars in females. Occasional specimens have extra pores or show only pore scars for the lateralmost positions of the row. The precloacal shield is twice as wide as deep and covered with six to eight, generally with six, segments, of which the median pair is the largest. The posterior rim of the cloaca is formed of eight to 14 irregular segments, with the median pair slightly or markedly enlarged. The lateral rows number two to four.

The tail is cylindrical and of slightly smaller diameter than the trunk. It increases in diameter posterior to the markedly constricted and narrowed autotomy annulus which falls on the sixth to ninth postcloacal caudal annuli. There are 18 to 24 caudal annuli up to the short, segmented tip. The last one or two interannular sutures are less deeply inscribed than the earlier ones. The distal tip of the tail lies at the caudal midline.

The lateral sulci are clearly marked after the twentieth to the fortieth body annuli. At midbody, their width is equal to or less than that of one of the bordering segments. There are no ventral sulci, but the dorsal sulci are indicated by the fringing rows of middorsal segments that are often slightly narrower than the adjacent dorsal elements.

At midbody the middorsal elements are one and one-half times as long as wide, and the proportions of the midventral ones vary from being twice as wide as long in juveniles to being one and one-quarter as wide as long in adults.

RANGE: Brazil, Rio Grande do Sul north to Espirito Santo, inland to Minas Gerais and Misiones, Argentina.

LOCALITY RECORDS: ARGENTINA: — M.A.C.N. No. 17839. *Misiones:* Oro Verde: N.M.B. No. 13364. Monte Carlo: C.N.H.M. Nos. 9323–9326. Leandro N. Alem: C.G. No. 1051.

BRAZIL: — M.C.Z. No. 5207; S.M.F. No. 11801; S.M.N.S. No. 2279. *Rio Grande do Sul:* — M.C.Z. Nos. 1021, 6338. "Im Urwalde": (Hensel, 1868); Z.M.U. Nos. 6828A, 6828B. Itaqui: D.Z. No. 6583. Santa Cruz do Sul: N.M.W. Nos. 12336:2–12336:40. Montenegro: (Cope, 1885); A.N.S.P. No. 12969 (holotype of *prunicolor*). Barão: C.N.H.M. Nos. 80104, 80105. Carlos Barbosa: C.N.H.M. No. 80103. Farroupilha: C.N.H.M. No. 80108; M.R.C.N. No. 987. Caxias do Sul: D.Z. Nos. 1921, 6581, 6606, 6609, 6666, 6921; M.R.C.N. Nos. 1079, 1080. Nova Petropolis: M.R.C.N. No. 2422; U.R.G.S. No. 628. Morro do Coco: C.N.H.M. No. 80107; D.Z. No. 6389. Pôrto Alegre: C.N.H.M. No. 80106; D.Z. Nos. 6390, 6391; H.M. No. 681; S.M.F. No. 21365; U.R.G.S. No. 631. Taquara (do Novo Mundo): N.M.B. No. 3811. *Santa Catarina:* — S.M.F. No. 11812. Nova Teutonia: S.M.F. Nos. 26464–26470; U.M.M.Z. No. 123127. *Paraná:* Foz de Iguaçu: M.N. No. 17546. ?Tijuca Preto, near Rio Negro: H.M. No. 2865E. Piraí: D.Z. No. 6444. *São Paulo:* Santo Anastacio: D.Z. No. 6632. Franca: D.Z. No. 6531. *Rio de Janeiro:* Porto Real: R.M.N.H. (unnumbered). *Minas Gerais:* São Cyprião: (Garman, 1883); M.C.Z. No. 5124. Juiz da Fora: K.M. No. R4448. *Espirito Santo:* Colatina: D.Z. No. 3507.

Amphisbaena prunicolor albocingulata
Boettger

Plate 43, figures 1–3; plate 44, figures 1–3; text figures 21–28, 40, 41

Amphisbaena albocingulata BOETTGER, 1885, p. 219. *Terra typica:* "Paraguay, Amer. merid." Holotype: Formerly Naturhistorisches Institut Linnaea, Frankfurt-am-Main, now Z.I.L. No. 6660.

DIAGNOSIS: A small-sized form of *Amphisbaena* without major fusions of head shields, with the prefrontals by far the largest segments on the dorsal, and the second infralabials on the ventral, surface of the head, with a relatively wide, elongate-appearing head that curves smoothly ventrad from the level of the frontals to the rostral tip, no intercalated half-annuli in the nuchal region, and with marked enlargement of the segments of the parietal and frontal regions. The form has 183 to 204 body annuli, 23 to 24 caudal annuli, a clearly marked autotomy site that falls on the seventh to ninth postcloacal annuli, 12 to 12.5 median numbers of dorsal and 15 to 18 median numbers of ventral segments to a midbody annulus, and four clearly marked, round, precloacal pores. The tip of the tail tends to lie at or above the caudal center line. Only the lateral sulci are marked, but the pair of dorsal rows flanking the midline has smaller segments. Specimens are light brown

dorsally, lighter ventrally. The pigment tends to drop out by segments on the ventral surface, in some cases over the entire region; in others only in restricted zones like the cloaca. Dorsal segments tend to show a central lightening of the otherwise even pigmentation.

DESCRIPTION: This is a small-sized form of *Amphisbaena*, with a light brownish, generally countershaded coloration. The fading of available individuals allows only an estimate of the actual coloration. The distribution of pigment is similar to that in the typical subspecies, though the color is generally lighter and the ventral surface more often has a wide clear zone. This light zone tends to be narrower posteriorly, but the cloacal region, specifically the cloacal shield, is often light. The ventral surface of the tail is pigmented. The dorsal segments characteristically show a very small, round, light-colored spot in the center. Since this is generally associated with a depression in the segmental surface, it is not clear whether it may represent a fixation artifact. The interannular and intersegmental raphes are light-colored.

The head segmentation is characterized by a lack of major fusions, by the very large prefrontal, the enlargement of the segments in the postocular and parietal regions, and the absence of postmalars and intercalated dorsal half-annuli from the nuchal region. In particular the postocular is of approximately equal size to the first parietal. The snout is relatively high, and the ventrad curvature starts in an even manner from the frontal-prefrontal suture. The temporal region is slightly, but noticeably, swollen; much of the swelling is directed laterally. There is scarcely any of the reverse curvature that characterizes the typical form. The lower jaw is generally deeper.

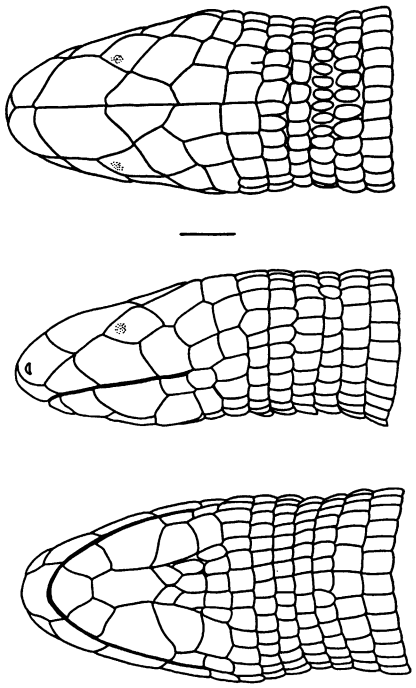


FIG. 40. *Amphisbaena prunicolor albocingulata*. Dorsal, lateral, and ventral views of the head of N.M.W. No. 12333:1 from "Paraguay-Linnaea." The line equals 1 mm. to scale. Drawn by V. Cummings.

The tip of the rostral is clearly visible in dorsal view. The general segmental pattern otherwise corresponds to that of smaller specimens of the typical form. There are generally two rows rather than one row of enlarged parietals. The postmental-postgenial region is narrower, and the infralabials and malars show a consequent shift in proportions. The first postgenial row has two to three segments. The smaller segments of the second row number three; from some specimens they are entirely absent. The "postmalar" row continues dorsally into the temporal-post-

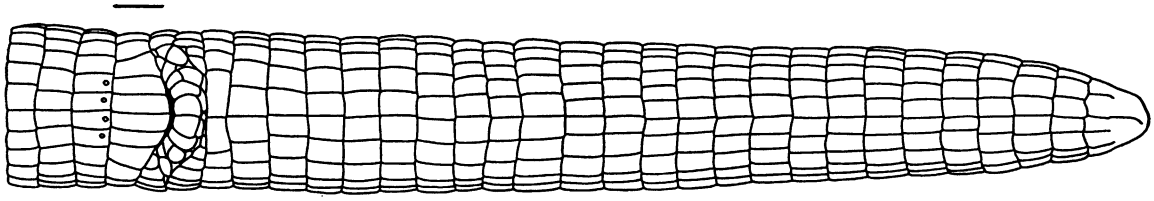


FIG. 41. *Amphisbaena prunicolor albocingulata*. Ventral view of cloaca and tail of N.M.W. No. 12333:1 from "Paraguay-Linnaea." The line equals 1 mm. to scale. Drawn by V. Cummings.

ocular sequence. Since these segments pass behind the angulus oris, they constitute the first body annulus. Neither the first nor the second body annulus shows any splitting of the enlarged segments in the nuchal region; there are then no intercalated dorsal half-annuli.

There are 183 to 204 body annuli, and annular irregularities are restricted to the cloacal region. A midbody annulus has a median count of 12 to 12.5 dorsal and 15 to 18 ventral segments.

The cloacal region is characterized by four round, variably expressed, precloacal pores. The precloacal shield has six to eight segments; the central six are generally enlarged. Laterals number three to four. The postcloacal rim includes 10 to 12 segments, of which the median pair is widest.

The tail shape is like that of the typical form. There are seven to nine annuli up to the autotomy site and a total number of 23 to 24 caudal annuli, not including the non-segmented tip.

Sulci and segment proportions are as in the typical form except that the ratios of segmental proportions are generally affected by the fact that this is a smaller form.

RANGE: Paraguay, from the borders of Misiones, Argentina, to Río Apa on the Brazilian frontier; possibly north into Mato Grosso and Goiaz, Brazil.

LOCALITY RECORDS: ARGENTINA: — M.A.C.N. No. 17840.

PARAGUAY: — N.M.W. Nos. 12333:1–12333:3; Z.M.V. No. 10618 (Rohde). Asunción: (Peracca, 1895); I.M.Z.U.T. No. 985. San Bernardino: U.M.M.Z. No. 103075. Río Apa: (Peracca, 1895); I.M.Z.U.T. Nos. 964A–964C.

BRAZIL: Districto Federal: ?Brasilia: C.G. No. 2808.

Amphisbaena hogei Vanzolini

Plate 43, figures 4–6; plate 44, figures 4–6; text figures 21–28, 42, 43

Amphisbaena darwini hogei VANZOLINI, 1950, p. 69. *Terra typica:* "Ilha dos Alcatrazes, S. P.," Brazil. Holotype: D.Z. No. 6905. Paratypes: D.Z. Nos. 6906–6920.

DIAGNOSIS: This is a small form of *Amphisbaena*, without major fusion of the head shields, with a bluntly pointed head, with the prefrontals by far the largest segments on the dorsal and the mental on the ventral surface of the head, with only slight swelling of the rostral tip but with considerable bulging of the temporal muscles, and a tendency to two enlarged pairs of parietal segments as well as general enlargements of the segments of the postocular region. The form has 177 to 191 body annuli, 15 to 19 caudal annuli, a clearly marked autotomy constriction that falls on the fourth to sixth (in one case on the seventh) postcloacal annulus, 10 to 13 dorsal and 14 to 18 median numbers of ventral segments to a midbody annulus, and four large, round, precloacal pores in both males and females. The tail is cylindrical and roundly capped distally. Only the lateral sulci are apparent. Specimens are brown dorsally and faintly countershaded. The central rectangle of each segment is more darkly pigmented; the pigmented area shrinks below the lateral line and finally drops out by segments.

DESCRIPTION: This small form of *Amphisbaena* has a light brownish dorsal and lighter ventral coloration. The dorsal surfaces of the head and tail are significantly darkened. The dorsal color is produced by a superficially even pigmentation of the individual segments. Upon closer inspection these appear to have a darker rectangular center which becomes more apparent because of the general lightening of the color along the sides. Here the pigment density and the pigmented area shrink in parallel, but the color ultimately drops out by segments. The ventral surface of the tail is faintly pigmented.

The head segmentation is characterized by lack of major fusions, by a tendency toward two pairs of parietals (the second pair may be split), by the enlargement of the segment in the postocular region, and by the high frequency (> 75%) of specimens with one rather than two postgenial rows. The snout is bluntly pointed and distally rounded and the prefrontal-nasal region is not particularly bent or swollen. There is some reverse curvature at the middle of the frontals, and the temporal muscle masses are moderately apparent. The rostral region projects only slightly beyond the shallow lower jaw. The neck is slightly constricted and then expands to the diameter of the regularly subcylindrical trunk which is scarcely thicker than the temporal zone. The tip of the rostral is

scarcely visible from above. Its ventral exposure is larger than that of the mental. Pairs of small nasals, very large prefrontals, medium-sized frontals, larger first and irregularly shaped second parietals follow in sequence along the dorsal surface of the head. The parietal region is often the site of irregularities and asymmetries. The posterior edge of the frontals corresponds approximately to the level of the angulus oris. There are three supralabials, but the posterior edge of the last generally lies anterior to that of the third infralabial; the posterior sutures form a continuous inclined line. The intersupralabial sutures run at angles of 20 degrees, 70 degrees, 80 degrees, and 60 degrees to the labial edge. The polygonal ocular is in contact with the second and third supralabials, and the prefrontals are in point contact with the frontals, and in more or less broad contact with one or two postoculars.

The mental is smaller than the large, as wide as long, polygonal postmental. The first infralabial is medium-sized, the second much larger, and the third very small. The malars are irregular; they may or may not be in contact with the postmental. A pair of (rarely three) large segments forms the first, and three to four tiny segments form the second, postgenial row, though the latter is lacking from more than 75 per cent of the material. There are six to eight postmalars; the lateralmost of these are usually widened. The segments of the gular region are very regular.

Dorsally the first body annulus divides once to form a single, anterior, dorsal half-annulus. The dorsal segments of this and the second body annulus comprise the enlarged elements of the temporal cover. The anterior suture of the third body annulus lies in a plane normal to the long axis of the trunk. The third through sixth annuli are slightly narrowed; the more posterior ones are of uniform length and lie more or less normally to the long axis of the trunk.

There are 177 to 191 body annuli from the back edge of the third infralabial up to and including the pore-bearing precloacal row. Intercalated dorsal half-annuli are rare, as are annular irregularities. A midbody annulus has median counts of 10 to 13 dorsal and 14 to 18 ventral segments. There is some segment irregularity between adjacent annuli.

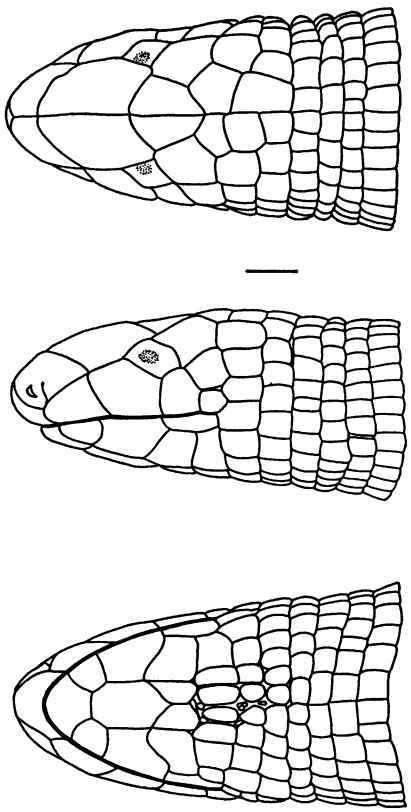


FIG. 42. *Amphisbaena hogei*. Dorsal, lateral, and ventral views of the head of S.M.F. No. 57904 from Ilha de Alcatrazes, São Paulo, Brazil. The line equals 1 mm. to scale. Drawn by V. Cummings.

The cloacal region is characterized by four large, evenly spaced, round, precloacal pores in both sexes. The precloacal shield is shallow, composed of six to eight segments, with the median pairs larger than the peripheral ones. The posterior edge of the cloaca is formed of eight to 12 segments, with the median pair the widest. There are two to four rows of laterals.

The tail is relatively short and cylindrical; it shows a gradual reduction in height and is capped by a rounded tip. The autotomy annulus is narrowed; it falls on the fourth to sixth (rarely on the seventh) postcloacal annuli. There is no autotomy constriction of the tail. The caudal annuli number 15 to 19, and only the last suture is weakly inscribed.

The lateral sulci are clearly marked after about the fiftieth body annulus; there is neither a dorsal nor a ventral sulcus.

At midbody the dorsal segments are slightly longer than wide; the ventral segments are slightly wider than long.

RANGE: The coast of Brazil from Santa. Catarina to São Paulo; islands of Queimada Grande and Alcatrazes.

LOCALITY RECORDS: BRAZIL: *Santa Catarina:* Joinville: N.M.W. No. 12337:6. *São Paulo:* Itapeva: D.Z. No. 3311. Boituva: D.Z. No. 6605. São Paulo: D.Z. Nos. 6633, 6634, 6675, 6691. ?São Bernardo dos Campos: D.Z. No. 6545. Ilha dos Alcatrazes: (Mertens, 1955; Vanzolini, 1950); D.Z. Nos. 1893, 1894, 6502–6512, 6692, 6905–6920 (type series of *hogei*), S.M.F. Nos. 57904–57907. Ilha Queimada Grande: S.M.F. Nos. 57908–57910.

Amphisbaena nigricauda, new species

Plate 45; text figures 21–28, 44, 45

HOLOTYPE: M.N. No. R3305, an adult female, collected on November 11, 1964, by F. M. Oliveira at the Refugio Sooretama, Linhares, Espirito Santo, Brazil.

PARATYPES: A.M.N.H. No. 97205, a juvenile; and C.G. No. 3207, an adult male; both collected with the holotype.

DIAGNOSIS: This is a small species of *Amphisbaena*, without major fusions of head shields, with the prefrontal the largest segment on the dorsal, and the second infralabial by far the largest segment on the ventral, surface of the head, with a strongly prognathous snout on the small head, enlarged postocular and parietal segments, no postmalar row, and a dark, pigmented, caudal tip. The form has 222 to 226 body annuli, 19 to 24 caudal annuli, a clearly marked autotomy annulus that falls on the sixth to ninth postcloacal annuli, 10 dorsal and 16 ventral segments to a midbody annulus, and four clearly marked, round pores in both sexes. The tail is cylindrical, with a conical distal tip. The coloration is very light brownish white, very slightly darker on the dorsal surface, but with the last six to eight caudal annuli much more heavily pigmented, both dorsally and ventrally. The darker pigment is produced by a speckling, rather than an even pigmentation of segments; the individual melanophores may be seen under the dissecting microscope.

DESCRIPTION: This is a small-sized species of *Amphisbaena* with a very light coloration. The anterior portion of the trunk shows no dark pigmentation. On the posterior two-thirds this appears by segments and descends on the sides to the vicinity of the lateral sulcus. The pigmentation of segments is produced by an even but open scattering of melanophores, giving the specimen a speckled appearance under the dissecting microscope. The distal tip of the tail is markedly darkened both dorsally and ventrally; here the pigment covers the segments more or less evenly. The light body color contrasted with the very dark caudal tip allows rapid recognition of this form.

The head segmentation is characterized by a lack of major fusions, by the very large prefrontal, and the enlargement of the postocular and the parietals. The snout is smoothly rounded in frontal and sagittal section; it is strongly prognathous, and the very shallow lower jaw is deeply inserted below the smallish head. The posterior portion of the head is horizontally oval. The temporal muscle masses are apparent but not particularly emphasized. The nuchal constriction is clear but short. The trunk is round to horizontally oval in cross section. It gradually in-

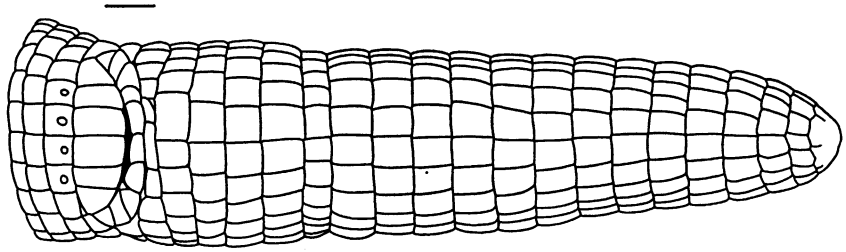


FIG. 43. *Amphisbaena hogei.* Ventral view of cloaca and tail of S.M.F. No. 57904 from Ilha de Alcatrazes, São Paulo, Brazil. The line equals 1 mm. to scale. Drawn by V. Cummings.

creases in diameter and does not achieve maximum proportion until midbody.

The rostral is almost entirely restricted to the ventral aspect of the snout; its tip is barely apparent in dorsal view. Pairs of medium-sized nasals, very large prefrontals, smaller frontals, of equal-sized first and only faintly enlarged second, parietals follow in sequence along the midline of the head. The segments of the parietal region appear symmetrical. The posterior edge of the frontal corresponds to the level of the middle of the third supralabial. There are three supralabials, but the postsupralabial is large. The first supralabial is the longest; the second occupies the greatest area. The labial sutures project at angles of 20 degrees, 50 degrees, 85 degrees, and 85 degrees in lateral view. The ocular is pentagonal; it is in broad contact with the second and third supralabials, and the prefrontal is in point contact with the frontal and lies posteriorly against two large (postocular) segments of the first body annulus.

The mental is elongate and wedge-shaped and lies in narrow, straight contact with the anterior edge of the lozenge-shaped postmental. The first infralabials are larger than the mental; the second are the largest segments on the lower jaw, and their contact distance with the postmental is approximately 160 per cent of that of the first. The third infralabials are much smaller. The anterior tips of the malar are not in contact with the postmental; their lateral tips touch the third infralabials along only part of their medial edges, being excluded from the rest by the enlarged postmalar segments of the first body annulus. There are two medium-sized

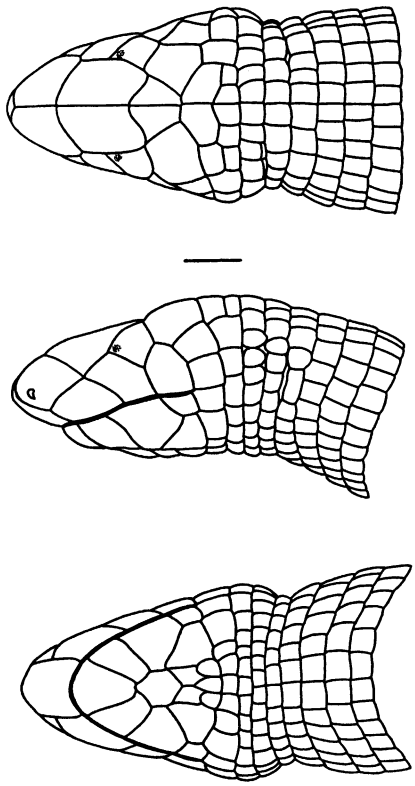


FIG. 44. *Amphisbaena nigricauda*. Dorsal, lateral, and ventral views of the head of paratype C.G. No. 3207, from Linhares, Espirito Santo, Brazil. The line equals 1 mm. to scale. Drawn by V. Cummings.

first, and three slightly smaller second, postgenials but no postmalars. The ventral segments of the first body annuli are regular.

Dorsally the first body annulus comprises three segments, the postsupralabial and first and second postoculars, each larger than the

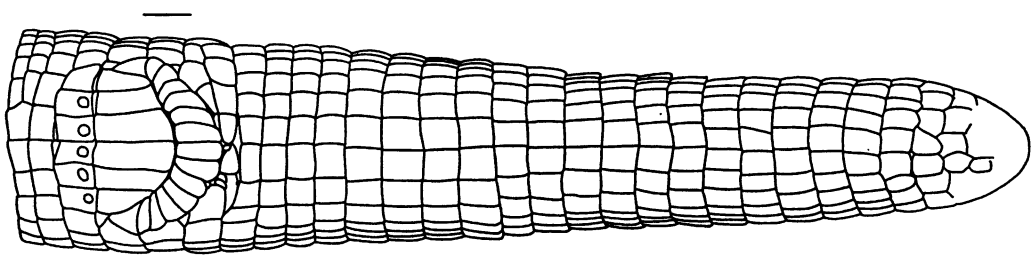


FIG. 45. *Amphisbaena nigricauda*. Ventral view of cloaca and tail of paratype C.G. No. 3207, from Linhares, Espirito Santo, Brazil. The line equals 1 mm. to scale. Drawn by V. Cummings.

one ventral to it. There are no intercalated dorsal half-annuli. The anterior edge of the fourth body annulus lies in a plane normal to the long axis of the trunk. The third, fourth, fifth, and sixth body annuli are narrowed and shorter; subsequent annuli are subequal.

There are 222 to 226 body annuli from the back edge of the third supralabial up to and including the pore-bearing precloacal row. There are no intercalated dorsal half-annuli, and irregularities are absent. A midbody annulus has 10 dorsal and 16 ventral segments. Segment irregularities are uncommon.

The cloacal region is characterized by four (one specimen has five) clearly marked, round pores in both males and females. The deep precloacal shield bears six segments, each longer than wide. The postcloacal edge is fringed by 10 to 13 segments, the sutures of which run more or less radially from the cloacal edge. The median pair is not significantly enlarged. The lateral rows number three to five.

The tail is cylindrical, slightly swollen beyond the autotomy constriction, and tipped with a gradually conical zone. The autotomy constriction falls on the sixth to ninth postcloacal annuli. There are 19 to 24 caudal annuli, the sutures between the last three being poorly inscribed.

The lateral sulci are clearly marked after the level of the fiftieth body annulus; at midbody they are slightly narrower than one of the bordering segments. Neither the dorsal nor the ventral sulcus is at all marked.

At midbody the middorsal elements are approximately as wide as long; the midventral segments are one and one-quarter as wide as long.

RANGE: Known from the types only.

Comments from the Literature

Behavior has been discussed by Mertens (1924, 1926) for terrarium specimens.

Pratt (1948) discussed the morphology of the nasal capsule, Fischer (1900) and Birabén (1954) commented on the eye, Richter (1933) described the hyoid and throat musculature, and Lynn and Komorowski (1957) described the thyroid. The lungs were described by Butler (1895) who also commented on the viscera and fat bodies (1889).

Ecological Problems Posed by the Findings

The preceding analysis attempts to characterize the species pattern from a combination of morphological and geographical information. Ecological data were specificially excluded and relegated to the next step in analysis. There they should provide a new and, presumably, independent line of evidence to test the present scheme. The kind of distribution pattern here shown, however, permits the posing of certain immediate problems; these deserve a statement and preliminary consideration.

The fundamental questions that may be asked are those basic to the study of animal distributions. They inquire why a form may occur in a particular region, what limits its range or has permitted its past extension, and how several similar forms compete or avoid competition in a particular area.

The distribution of an amphisbaenid may in its broadest terms be considered to be affected by three categories of factors: the nature and abundance of food organisms, the nature and perhaps the humidity regime of the substratum, and the climatic factors (e.g., temperature, rainfall) *per se*. The obvious lack of ecological data for all but a few localities forces emphasis on evidence from distribution patterns and from the nature of the polytypic variation. The present discussion, then, may be considered only as a guide for additional tests.

Klappenbach's (1960) demonstration of the ecological separation of *A. darwini* and *A. munoai* in Uruguay furnishes a first-level key. *Amphisbaena darwini*, the larger species, is there distributed widely across an apparently continuous zone of more or less open country. The smaller species appears to have a discontinuous range; it is restricted to a series of low, but sharply defined, wooded ranges that rise from the lowland plains. Klappenbach has suggested (personal communication) that *A. munoai* is a form of the immediate subsurface zone; it is taken at shallow depths, under surface rocks in wooded areas. The two forms occupy the same zone only along the bases of the hills, and perhaps on hills that have been denuded of vegetation. *Anops kingi*, the third species of this zone, apparently shares the general habitat of *A. darwini*, though there are suggestions (cf. Birabén, 1954) that it may be the exclusive inhabitant of harder and more compacted soils.

Unfortunately there is no similar key to the ecological situation in Rio Grande do Sul. The samples of *A. darwini* again come from a wide scattering of localities. The north-coastal samples (Osorio, Tramandaí) were taken at depths of from 30 to 60 cm. in plowed, sandy fields and from the root stocks of trees, cacti, and large bushes growing along their margins. The sympatric *Anops kingi* reaches its northern limit in this zone. There are no ecological data for *darwini* from more inland areas (where specimens show the markedly tuberculate tails), nor is there such information for the northern records of *A. munoai*. Localities for *A. p. prunicolor* are commonest in the more tropical, moist, forested hills that once extended across the northern portion of this state, and there is Hensel's (1868) comment that specimens collected by him (and later identified as *A. p. prunicolor*) were taken "im Urwalde." The localities from which "lead-phase" specimens are recorded are also from within this forest zone.

No ecological information exists for populations from more western and northern regions. *Amphisbaena darwini* occupies the coastal region in Rio Grande do Sul and Santa Catarina but seems not to occur on the lowland coastal strip in São Paulo. Similarly *A. hogei* which exists on at least two small is-

lands off the coast may also be absent from the coastal strip; certainly all mainland localities seem to be on or inland of the coastal mountains.

The scarcity of northern records does not indicate lack of collecting or scarcity of amphisbaenids. The species of the present grouping, or groupings, in this area are in the inland zone more or less sympatric with *Amphisbaena alba*, *dubia*, *mertensi*, and *roberti*, and very large series of several large forms of *Leposternon* are available from both the coastal strip and the more inland localities. The total number of localities, samples, and specimens, and for that matter of species, is greater, but the relative density is much less.

The pattern suggests that the various species of amphisbaenids may well be in direct competition for food and for their rather specialized habitat. There may even be more direct interaction of these formidable predators. Numerous unpublished observations indicate that specimens of some of these species will (in captivity) bite each other when crowded (or even during random encounters) and that the larger forms will eat smaller ones.

As suggestive is the shift in body size of the polytypic forms. *Amphisbaena darwini* reaches its largest size in São Paulo and Paraná, where it is sympatric with the smaller forms, *A. hogei*, *prunicolor*, *and roberti*, and the medium-sized *A. dubia*. (It is unclear how the larger *A. mertensi* fits into this picture. Does it replace *A. darwini* in Misiones and eastern Paraguay?) In contrast, *A. darwini* is smaller in Uruguay, where there seems good ecological separation versus the small *A. munoai*. In Argentina, where it is widely sympatric only with the much larger *A. angustifrons* and *A. camura*, and where there is no smaller species of the genus, *A. darwini* shows the smallest total size.

The relatively heavy jaws, solid and interlocking dentition, and powerful temporal and axial musculature of the amphisbaenians are combined with special feeding mechanisms and habits. They permit these animals to cope even with relatively large prey. The kind of food item utilized is then a function more of the animal's behavior pattern than of the structure of its feeding mechanism. Laboratory observations suggest that the several species here discussed are highly nonselective feeders. Specimens of a single species have, for instance, taken insects of a number of stages and orders, other small arthropods, and various annelids. The large amphisbaenians (*Amphisbaena alba*, *A. camura*) also accept reptiles and mammals (almost fully grown mice). At least two of the larger species have been kept in zoos for several years on a diet of frozen smelt (S. Spencock, personal communication).

It is possible to predicate an advantage for an animal that is able to achieve sexual maturity at a smaller total size for otherwise identical conditions. The advantage consists in allowing the population to be composed of a greater number of individuals for a given food supply, or even a greater number of individuals to a particular volume of substratum. A different advantage to a burrowing form might be the smaller body diameter for an equivalent body size. Increased burrowing effectiveness might also be obtained by a modification of the head shape or of the force-application pattern, but size changes may be easier to achieve on a given genetic background.

Size changes, however, may have numerous other effects, as, for instance, on the predation pressure the population may have to bear. Furthermore, they affect the capacity to utilize different size and activity classes of food objects. As the relative size of food particles decreases, so presumably does the food-gathering effectiveness. An increase in the relative size of food objects mainly involves an increase in the defensive capacity of the prey. Amphisbaenid intestines often contain portions of the exoskeleton of arthropods that must have been larger than the head of the amphisbaenid, and I have observed *A. camura* killing and biting chunks out of a mouse that was twice its diameter. The upper limit may thus not be as fixed for amphisbaenids as for snakes, which must swallow their prey whole. The combination of observations suggests mechanisms for establishing the advantages that seem to have channeled population genotypes in the diection of small body size.

Another aspect that becomes ever more clear is that amphisbaenians have been far

more successful at invading coastal, and even oceanic, islands than would have been predicted from a superficial consideration of their mode of life history. In the present study they have been recorded from four sets of islands, the two off the coast of São Paulo being relatively small and far out in the open ocean. Various islands off the coast of São Paulo and Rio de Janeiro sustain very dense populations of *Leposternon* (P. E. Vanzolini, personal communication), while the oceanic island of Fernando da Noronha (Brazil) is occupied by the distinct and endemic species *Amphisbaena ridleyi*. Some 11 species of *Cadea* and *Amphisbaena* are found on the islands of the northern Caribbean. *Cynisca leonina* reaches the Los Archipelago (Guinea), and *Blanus s. strauchi* reaches various islands in the eastern Mediterranean. The island populations are often remarkably similar to those on adjacent islands or on the mainland, as is shown in the four cases recorded in the present paper. A very similar situation exists in *Blanus cinereus*, the range of which extends from Spain and Portugal into Maroc, though the line of major intraspecific diversification seems to fall between Tanger and Maroc (cf. Bons, 1963) rather than at the strait of Gibraltar. These examples suggest that we are far from understanding the bases for variation in these animals. Furthermore, they imply the utility of intensive studies of populations on coastal islands, such as those along the coast of southeastern Brazil.

The above considerations are presented only as suggestions toward possible approaches. Needed are adequate ecological information, and parallel studies of the actual food preferences of the animals, of the physical constants of the soils within which they dig, and of the fundamental parameters of their physiology. Such aspects may then be correlated with their structural and behavioral specializations. Study of them forms a logical succession to the present preliminary characterizations of the species patterns.

LITERATURE CITED

ALEXANDER, A. ALLAN

1966. Taxonomy and variation of *Blanus strauchi*, with comments on the nature of its meristic variation. Copeia, no. 2, pp. 205–224.

ALEXANDER, A. ALLAN, AND CARL GANS

1966. The pattern of dermal-vertebral correlation in snakes and amphisbaenids. Zool. Meddel., Leiden, vol. 41, no. 11, pp. 171–190.

AMARAL, AFRANIO DO

1935. Um novo genero e duas novas especies de geckonideos e uma nova raca de amphisbaenideo, procedentes do Brasil central. Mem. Inst. Butantan, vol. 9, pp. 253–256.

1937. Estudos sobre lacertilios neotropicos. 4. Lista remissiva dos lacertilios do Brasil. *Ibid.*, vol. 11, pp. 167–204, i–ix.

BIRABÉN, MAX

1954. El ojo anópsico de anfisbénidos argentinos. Physis, vol. 20, no. 59, pp. 390–396.

BOETTGER, OSKAR

1885. Liste von Reptilien und Batrachien aus Paraguay. Zeitschr. Naturwiss., ser. 4, vol. 58, no. 3, pp. 213–248.

1893. Katalog der Reptilien-Sammlung im Museum der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt-am-Main. Frankfurt-am-Main, pp. i–ix, 1–140.

BONS, JACQUES

1963. Notes sur *Blanus cinereus* (Vandelli). Description d'une sous-espèce marocaine: *Blanus cinereus mettetali* ssp. nov. Bull. Soc. Sci. Nat. Phys. Maroc, vol. 43, pp. 95–107.

BOULENGER, GEORGE ALBERT

1885a. Catalogue of the lizards in the British Museum (Natural History). Second edition. London, vol. 2, xiii+497 pp.

1885b. Remarks on a paper by Prof. E. D. Cope on the reptiles of the Province Rio Grande do Sul, Brazil. Ann. Mag. Nat. Hist., ser. 5, vol. 16, pp. 294–298.

BURMEISTER, HERMANN

1861. Reise durch die La Plata-Staaten mit besonderer Rücksicht auf die physische Beschaffenheit und den Culturzustand der Argentinischen Republik. Ausgeführt in den Jahren 1857, 1858, 1859 und 1860. Halle, vol. 1, vi+503 pp.; vol. 2, vi+540 pp.

BURT, CHARLES E., AND MAY DANHEIM BURT

1930. The South American lizards in the collection of the United States National Museum. Proc. U. S. Natl. Mus., vol. 78, pp. 1–52.

1933. A preliminary check list of the lizards of South America. Trans. Acad. Sci. St. Louis, vol. 28, no. 1, pp. i–vi, 1–104.

BUTLER, GERARD W.

1889. On the relations of the fat bodies of the Sauropsida. Proc. Zool. Soc. London, pp. 602–613.

1895. On the complete or partial suppression of the right lung in the Amphisbaenidae and of the left lung in snakes and snake-like lizards and amphibians. *Ibid.*, pp. 691–712.

COPE, EDWARD DRINKER

1885. Twelfth contribution to the herpetology of tropical America. Proc. Amer. Phil. Soc., vol. 22, pp. 167–194.

DEVINCENZI, GARIBALDI J.

1925. Fauna erpetológica del Uruguay. An. Mus. Hist. Nat. Montevideo, ser. 2, vol. 2., pp. 1–65.

DUMÉRIL, ANDRÉ MARIE CONSTANT, AND GABRIEL BIBRON

1839. Erpétologie générale ou histoire naturelle complète des reptiles. Paris, vol. 5, 855 pp.

DUMÉRIL, AUGUSTE HENRI ANDRÉ (not Duméril, André Marie Constant, and Auguste Henri André Duméril)

1851. Catalogue méthodique de la collection des reptiles du Muséum d'Histoire Naturelle de Paris. Paris, iv+224 pp.

FISCHER, EUGEN

1900. Beiträge zur Kenntniss der Nasenhöhle und des Tränennasenganges der Amphisbaeniden. Arch. Mikros. Anat. Entwicklungsgesch., vol. 55, pp. 441–478.

FREIBERG, MARCOS A.

1939. Enumeracíon sistemática de los reptiles de Entre Rios y lista de los ejemplares que los representan en el Museo de Entre Rios. Mem. Mus. Entre Rios, Zool., no. 11, pp. 1–28.

GANS, CARL

1959. A taxonomic revision of the African snake genus "Dasypeltis" (Reptilia: Serpentes). Ann. Mus. Roy. Congo Belge, ser. in 8°, Sci. Zool., vol. 74, pp. 1–237.

1960. Studies on amphisbaenids (Amphis-

baenia, Reptilia). 1. A taxonomic revision of the Trogonophinae, and a functional interpretation of the amphisbaenid adaptive pattern. Bull. Amer. Mus. Nat. Hist., vol. 119, art 3, pp. 129–204.

1962. Notes on amphisbaenids (Amphisbaenia, Reptilia). 6. Range extension and redescription of *Amphisbaena spurrelli* Boulenger. Breviora, no. 171, pp. 1–11.

1964a. A redescription of, and geographic variation in, *Liophis miliaris* Linné, the common water snake of southeastern South America. Amer. Mus. Novitates, no. 2178, 58 pp.

1964b. On the South American *Amphisbaena* with a vertically keeled tail. [Notes on amphisbaenids 15]. Senckenbergiana, vol. 45, nos. 3–5, pp. 387–416.

1965. Notes on amphisbaenids (Amphisbaenia, Reptilia). 17. A redescription and discussion of *Amphisbaena angustifrons* Cope and *Amphisbaena camura* Cope of southern South America. Amer. Mus. Novitates, no. 2225, pp. 1–32.

[In press.] Amphisbaena mildei Peters, 1878 (Reptilia): Proposed suppression under the plenary powers. Z.N. (S.) 1746. Bull. Zool. Nomenclature.

[MS.] A check list of recent amphisbaenians (Amphisbaenia, Reptilia).

GANS, CARL, AND A. ALLAN ALEXANDER

1962. Studies on amphisbaenids (Amphisbaenia: Reptilia). 2. On the amphisbaenids of the Antilles. Bull. Mus. Comp. Zool., vol. 128, no. 3, pp. 65–158.

GANS, CARL, CHESTER HUANG, AND FRED H. CLARK

[MS.] The polyphyletic origin of the amphisbaenids: A reevaluation based upon chromosome counts.

GANS, CARL, AND CHARLYN RHODES

[MS.] Chirindia from Tanganyika (Amphisbaenia: Reptilia). [Notes on amphisbaenids 19]. Ann. Carnegie Mus.

GARMAN, SAMUEL

1883. On certain reptiles from Brazil and Florida. Sci. Observer, Boston, vol. 4, no. 5–6, pp. 47–48.

GOELDI, EMILIO

1902. Lacertilios. Lagartos do Brazil. Bol. Mus. Paraense, vol. 3, no. 3–4, pp. 499–560.

HELLMICH, WALTER

1960. Die Sauria des Gran Chaco und seiner Randgebiete. Abhandl. Bayerischen Akad. Wiss., Math. Nat. Kl., new ser., no. 101, 131 pp.

HENSEL, REINHOLD

1868. Beiträge zur Kenntniss der Wirbelthiere Südbrasiliens. (Part.) Arch. f. Naturgesch., pp. 323–375.

IHERING, HERMANN VON

1898. Contributions to the herpetology of São Paulo, Brazil—I. Proc. Acad. Nat. Sci. Philadelphia, pp. 101–109.

KLAPPENBACH, MIGUEL A.

1960. Notas herpetologicas, I. *Amphisbaena muñoai* n. sp. (Amphisbaenidae). Comm. Zool. Mus. Hist. Nat. Montevideo, vol. 4, no. 84, pp. 1–12.

KOSLOWSKY, JULIO

1895. Reptiles y batracios de la Sierra de la Ventana (Provincia de Buenos Aires). Rev. Mus. La Plata, vol. 7, no. 1, pp. 149–156.

LYNN, W. GARDNER, AND LOUIS A. KOMOROWSKI

1957. The morphology of the thyroid gland in lizards of the families Pygopodidae and Amphisbaenidae. Herpetologica, vol. 13, no. 3, pp. 163–172.

MAYR, ERNST

1954. Change of genetic environment and evolution. *In* Huxley, Julian, A. C. Hardy, and E. B. Ford (eds.), Evolution as a process. London, George Allen and Unwin Ltd., pp. 157–180.

MERTENS, ROBERT

1924. Beobachtungen an *Amphisbaena darwini* D. and B. in Gefangenschaft. Bl. Aquar. Terr. Kunde, vol. 35, no. 8, pp. 1–2.

1926. Wieder andere Froschlurche und eine Eidechse aus Porto Alegre, Süd-Brazilien. *Ibid.*, vol. 37, no. 7, pp. 73–77.

1955. Eine brasilianische Inselfahrt. 1. Queimada Grande, die Insel der Giftschlangen. Natur und Volk, vol. 85, no. 10, pp. 305–314.

MÜLLER, FRITZ

1885. Erster Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. Verhandl. Naturf. Gesell. Basel, vol. 7, pp. 120–165.

MÜLLER, LORENZ

1941. Über die in der Sammlung des Zoologischen Institutes der Universität Halle a. Saale aufbewahrten Amphibien und Reptilientypen. Zeitschr. Naturwiss., vol. 94, pp. 182–205.

NÁGERA, JUAN JOSÉ

1915. Batracios y reptiles de la Sierra Baya. Physis, vol. 2, no. 9, pp. 23–30.

PARKER, HAMPTON WILDMAN

1928. A new species of lizard from Argentina.

Ann. Mag. Nat. Hist., ser. 10, vol. 2, pp. 383–384.

PERACCA, MARIO GIACINTO
1895. Viaggio del dott. Alfredo Borelli nella Repubblica Argentina e nel Paraguay. X. Rettili ed Anfibi. Boll. Mus. Zool. Univ. Torino, vol. 10, no. 195, pp. 1–32.
1897. Viaggio del Dott. Alfredo Borelli nel Chacco boliviano e nella Repubblica Argentina. II. Rettili ed Anfibi. *Ibid.*, vol. 12, no. 274, pp. 1–19.

PETERS, WILHELM CARL HASKINS
1878. Über vier neue amerikanische *Amphisbaena*-Arten. Monatsb. Akad. Wiss. Berlin, pp. 778–781.

PRATT, C. W. MCE.
1948. The morphology of the ethmoidal region of *Sphenodon* and lizards. Proc. Zool. Soc. London, vol. 118, pp. 171–201.

RICHTER, HERBERT
1933. Das Zungenbein und seine Muskulatur bei den Lacertilia vera. Jenaische Zeitschr. Naturwiss., new ser., vol. 59, pp. 395–480.

STOLL, N. R., AND OTHERS (EDS.)
1961. International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology. London, xviii+176 pp.

STRAUCH, ALEXANDRE
1881. Bemerkungen über die Eidechsenfamilie der Amphisbaeniden. Mel. Biol. Acad. Imp. Sci. St. Pétersbourg, vol. 11, pp. 355–479. *Reprinted:* 1881, Bull. Acad. Imp. Sci. St. Pétersbourg, vol. 28, cols. 45–131.

THOMAS, RICHARD
1965. Two new subspecies of *Amphisbaena* (Amphisbaenia, Reptilia) from the Barahona Peninsula of Hispaniola. Breviora, no. 215, pp. 1–14.

VANZOLINI, PAULO EMILIO
1949. Contribuições ao conhecimento dos lagartos brasileiros da familia Amphisbaenidae Gray, 1825. 3. Sobre *Amphisbaena vermicularis centralis* Amaral, 1935. An. Paulistas Med. Cirurgia, vol. 57, no. 2, pp. 105–108.
1950. Contribuições ao conhecimento dos lagartos brasileiros da familia Amphisbaenidae Gray, 1825. I. Sobre uma nova subspecies insular de *Amphisbaena darwinii* D. and B., 1839. Papéis Avulsos Dept. Zool., São Paulo, vol. 9, pp. 69–77.
1951. *Amphisbaena fuliginosa*. Contribution to the knowledge of the Brazilian lizards of the family Amphisbaenidae Gray, 1825. 6. On the geographical distribution and differentiation of *Amphisbaena fuliginosa* Linné. Bull. Mus. Comp. Zool., vol. 106, no. 1, pp. 1–67.
1953. On the type locality of some Brazilian reptiles and amphibians collected by H. H. Smith and described by E. D. Cope. Copeia, pp. 124–125.
[MS.] Evolution, adaptation and distribution of the amphisbaenid lizards (Sauria: Amphisbaenidae). Cambridge, Massachusetts, thesis submitted to Harvard University, 1951, 148 pp.