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Description and Geographical Variation of the South American *Amphisbaena angustifrons*: the Southernmost Amphisbaenian in the World (Reptilia, Amphisbaenia)

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ABSTRACT

The species *Amphisbaena angustifrons* Cope is reappraised on the basis of new specimens from southern South America. *Amphisbaena plumbea* Gray is treated as a race of *angustifrons* because of the occurrence of specimens from La Pampa, Argentina, intermediate in character pattern.

INTRODUCTION

In 1872 Gray described *Amphisbaena plumbea* based on a single specimen apparently broken at midbody. The name has been referred to several times in the literature, but reference has been generally to specimens of different species. Koslowsky's (1898, p. 187) record refers to *Amphisbaena angustifrons* and *A. darwini heterozonata*, whereas Amaral (1935), in synonymizing this form with "*Amphisbaena vermicularis darwini*," managed to confound three quite unrelated species. Parker (1928) appeared to have been correct in stating that this form was "closely allied" (= externally

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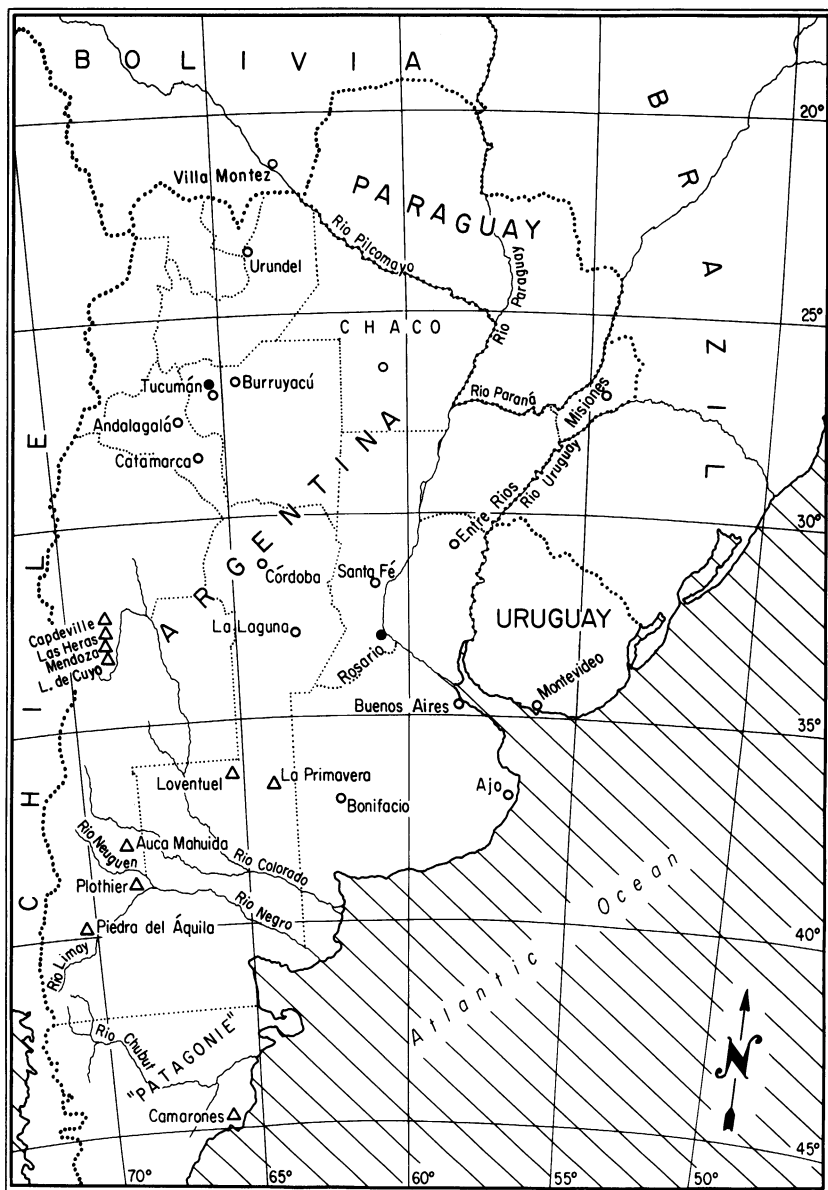


Fig. 1. Map of localities mentioned in text. Open circles refer to localities for specimens of *Amphisbaena angustifrons angustifrons* described in Gans (1965). Dots refer to new localities for *A. a. angustifrons*. Triangles refer to localities for *A. a. plumbea*.

similar) to his *Amphisbaena knighti* (= *angustifrons* Cope, 1861) but not in assuming an equivalent similarity to *A. darwini*.

It is now possible to redescribe *Amphisbaena plumbea* and to extend its range south from Mendoza to Camarones in Patagonia. In carrying out this analysis it became very clear that the three specimens of *angustifrons* (from Mendoza and Neuquén), noted earlier (Gans, 1965) as being aberrant as they had significantly higher numbers of body annuli, belong to *A. plumbea*, as all three possess a definite intravertebral autotomy plane which is missing in typical *A. angustifrons*. Three specimens from La Primavera, La Pampa, are apparently intermediate in various characteristics and remain a problem in the present study. In view of the existence of intermediate characteristics in specimens from a geographically intermediate area, it seems appropriate to redescribe *Amphisbaena plumbea* as a race of *Amphisbaena angustifrons*.

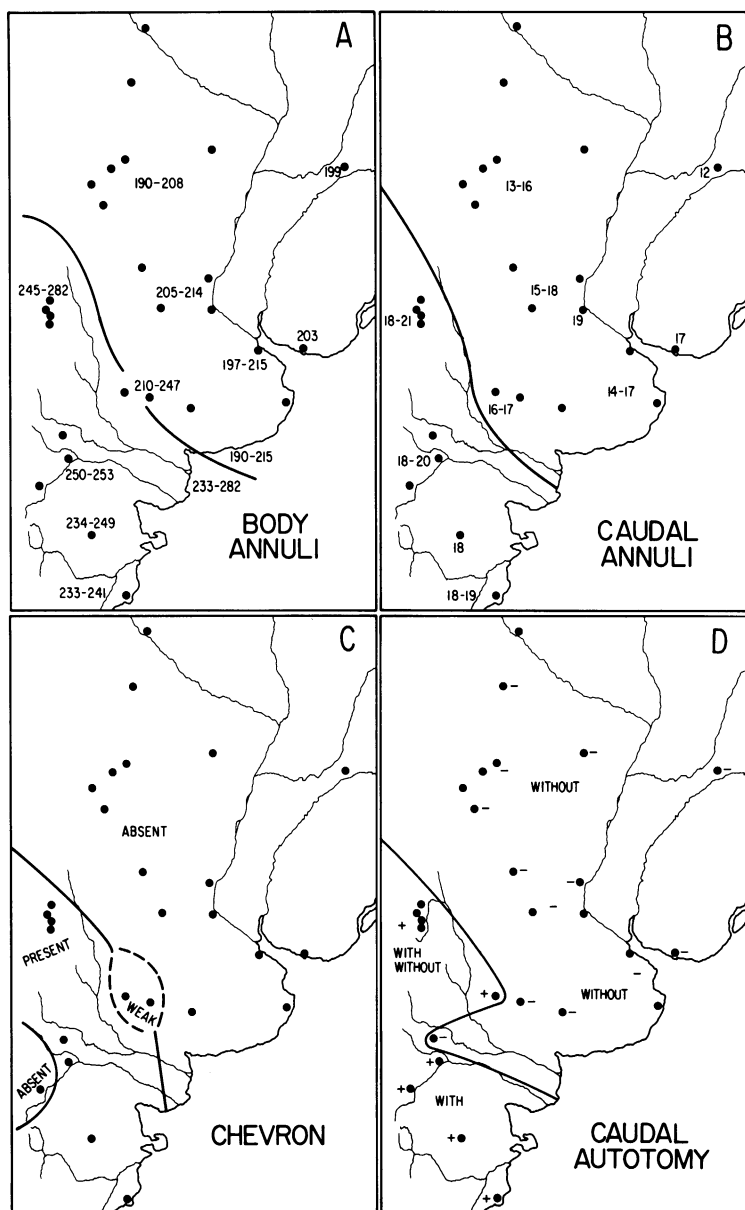
The present paper furnishes a standardized (Gans, 1966) redescription of this race based upon an examination of five new specimens of *Amphisbaena angustifrons angustifrons* and 15 specimens of *Amphisbaena angustifrons plumbea* including the type. The material examined came from the collection of the following institutions (identified throughout by the abbreviations in parentheses), and we are grateful to those persons in charge of collections who lent the specimens employed in this investigation: the American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); British Museum (Natural History), London (BM); Carl Gans personal collection (CG); Instituto de Biología, Mendoza, Argentina (IBM); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (MACN); Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ); Muséum National d'Histoire Naturelle, Paris (MHNP); Naturhistorisches Museum, Basel, Switzerland (NMB); Naturhistorisches Museum zu Wien, Austria (NMW); Rijksmuseum voor Natuurlijke Histoire, Leiden, Holland (RMNH); National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM); R. Sage personal collection, University of Texas, Austin (SC); Zoologische Sammlung des Bayerischen Staates, Munich, Germany (ZSM). Miss Jenny A. Cochrane figured the specimen and Mr. J. A. Stamos drew the maps. This study is supported by Grant GB-6521X from the National Science Foundation.

GEOGRAPHICAL VARIATION

This study refers to new records of *Amphisbaena angustifrons* from the Argentinian provinces of Santa Fé and Tucumán (see fig. 1 for localities and table 1 for data). The specimens of *Amphisbaena angustifrons plumbea*

TABLE I
DATA FOR ADDITIONAL SPECIMENS OF *Amphisbaena angustifrons*

Museum Number	Body, Lateral and Caudal Annuli	Dorsal and Ventral Segments	Labials	Chin Segments	Cloaca	Total Length (mm.)	Midbody Diameter (mm.)
ZSM 43/1918A	204+4/3+19	23-24+25	4/3	2+3+9	4+6+14	240+31	11.5
ZSM 43/1918B	218+4+19	22-23+25	4/3	2+4+11	4+6+14	255+29	11.0
CG 3568	199+3+14	25+28	4/3	2+4+12	4+6+15	240+25	12.0
CG 4948	204+4+14	25+30	4-3/3	2+3+9	4+6+15	338+36	16.3
CG 4949	207+3+14	28+36	4/3	3+5+11	4+8+16	365+30	17.0
RMNH (Unnumbered)	233+3+(6)17	26+25	4/3	2+5+8	4+6+14	164+15	6.2
NMB 6268	235+4+(7)18	22+26	4/3	2+5+11	4+8+16	283+32	10.3
NMB 6269	241+4+(7)18	25+25	3/3	2(2)+8+13	4+8+16	224+20	8.0
NMB 6270	233+5+(7)19	24+26	3/3	2+7+12	4+8+14	100+11	4.0
MHNP 00:31	234+4+(5)18	20+22	4/3	2+5+9	4+6+13	237+22	7.4
MHNP 00:32	249+4+6+x	26-27+26	4/3	2+6+11	4+6+14	197+7	6.0
MACN 7916	223+4+17	20+24-25	4/3	2+5+11	4+6+14	268+25	12.0
MACN 7917	210+3/4+16	23+24	4/3	2+5+10	4+6+15	197+20	8.0
MACN 7918	220+3+17	27+27-28	4/3	2+5+12	4+8+13	235+25	10.0
MACN 7196	247+5+(7)17	21+26	3/3	2+5+10	4+6+16	235+23	7.0
BM RR1946.8.2.7	254+4+(7)20	20+26	3/3	2+4+9	4+6+13	203+21	—
USNM 52971	274+4+(7)21	22+24	4/3	2+4+10	4+7+14	232+21	5.2
MCZ 15914	268+4+(7)21	20+22-23	3/3	2+4+9	4+6+13	202+20	5.0
IBM 0134R	262+4+(7)18	18-20+22-24	4/3	2+5+9	4+6+16	278+26	8.6
IBM 0180R	282+3+(9)21	18-20+20	3-4/3	2+5+11	4+6+14	172+18	4.0
MACN 17878	245+4+18	24+30	4/3	2+5+10	4+8+16	273+26	9.0
SC (Unnumbered)	282+3+(8)20	20+26	4/3	2+5+10	4+7+15	238+22	6.0
MACN 7976	253+4+18	24+26	4/3	2+5+12	4+8+14	223+22	8.0
MACN 10262	250+4+18	22-24+24	4/3	2+6+14	4+8+13	217+22	9.0
NMW 8	251+5+(6)20	22+22	4/3	2+4+9	4+6+12	228+24	6.5



came from the Argentinian provinces of Mendoza, La Pampa, Neuquén, and Chubut, as well as from "Patagonie" without specific locality. The specimens from Chubut were collected at Camarones almost at latitude 45° S; this is by far the closest that this order comes to either pole since the Recent amphisbaenids have a narrower latitudinal range than the other two orders of Squamata. In the Northern Hemisphere the limit is now set around 42° N, being represented by the genus *Blanus* in the Iberian Peninsula (Gans, 1967a). In Africa *Monopeltis capensis* reaches the Cape Province (32° S). Fossil amphisbaenians are known to occur from the Tertiary up to latitude of 45° N in North America (Gans, 1967b) and to 51° N in Europe (Belgium, Hochstetter, *in litt.*).

The amphisbaenians reflect the general pattern of diversity in that the number of genera and species decreases away from the tropics. We still lack a clear hypothesis to explain their actual distribution, although temperature, humidity, and soil type may play the main role in amphisbaenian zoogeography.

When the number of body annuli is plotted for the entire assemblage (fig. 2A), a sharp break is noted between the samples north and northeast of a line connecting the southwestern parts of the provinces of Buenos Aires and Tucumán ($R=190-215$) and those from Mendoza, Neuquén, and the southern regions ($R=233-282$). Only the samples from the region of La Pampa show intermediacy in these characteristics ($R=210-247$).

With the exception of the sample from Santa Fé (including two specimens with counts of 19) the numbers of caudal annuli from north of the Tucumán-Buenos Aires line ($R=12-17$) show a clear nonoverlap from those of the specimens from Mendoza, Neuquén, and Chubut ($R=18-21$). The specimens from La Pampa ($R=16-17$) clearly fall into the more northern grouping (fig. 2B).

Typical *Amphisbaena angustifrons* was described as lacking externally apparent caudal autotomy. Nevertheless, Alexander (1966) mentioned a specimen (from General Pico, La Pampa) that lacked an external autotomy constriction but showed a vertebral autotomy plane. The present analysis confirms that all specimens from north of the Tucumán-Buenos Aires line lack an externally apparent autotomy constriction (figs. 6 and 10 in Gans, 1965). Such a constriction is also lacking in one out of five specimens from Mendoza, in all specimens from La Pampa (fig. 3), and in the specimen from Auca Mahuida, Neuquén. All other individuals have more or less clearly defined autotomy annuli (fig. 4).

The presence of a vertebral autotomy plane is clearly notable on lateral and vertical X-rays (figs. 5, 6). A check of the available specimens (fig. 2C) indicates that all individuals from north of the Buenos Aires-Tucumán

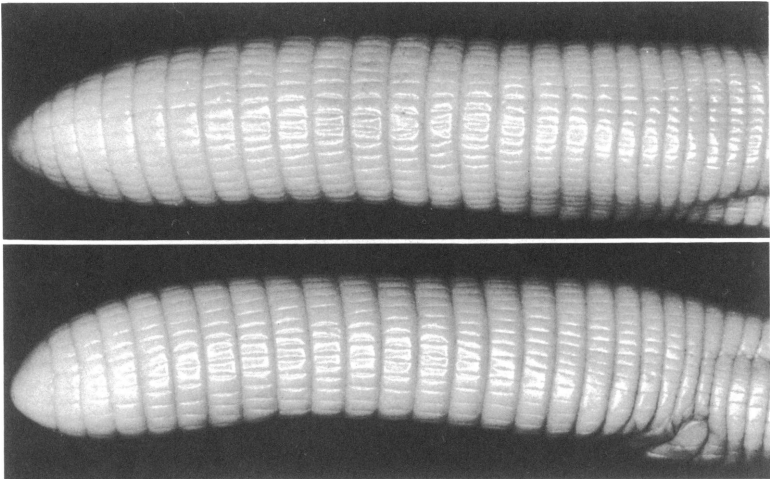


FIG. 3. *Amphisbaena angustifrons plumbea*, dorsal and lateral view of tail of MACN 7196, from Loventuel, La Pampa. Notice lack of an autotomy constriction or narrowing.

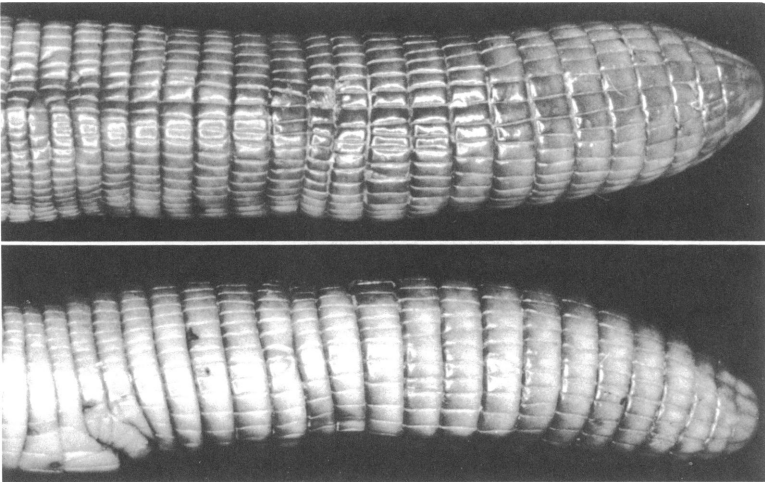


FIG. 4. *Amphisbaena angustifrons plumbea*, dorsal and lateral view of tail of MHNP 0031, from "Patagonie." Notice autotomy site at fifth caudal annulus.

line lack any trace of a vertebral autotomy plane but that such a plane occurs in specimens from the south and west, whether or not the tail has

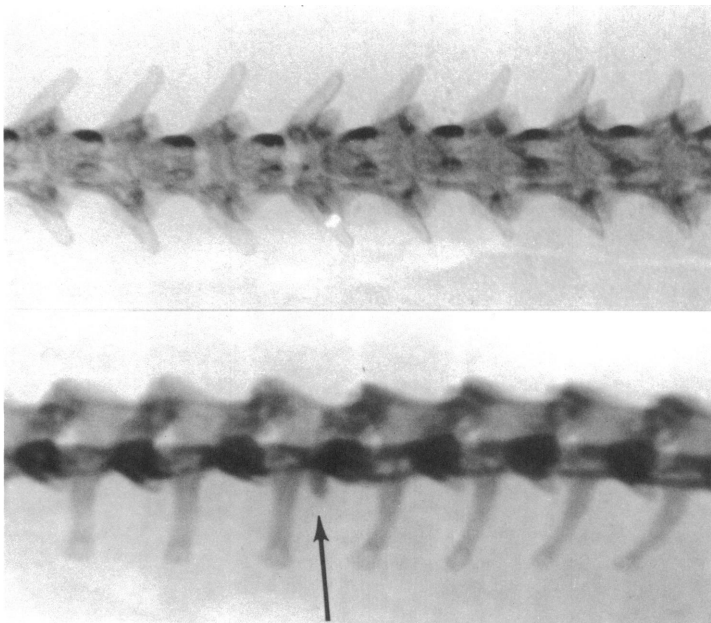


FIG. 5. *Amphisbaena angustifrons plumbea*, dorsal and lateral X-ray view of caudal vertebrae of MACN 7196, from Loventuel, La Pampa. Notice that this specimen which lacks external constriction has a vertebral fracture plane and protruding haemapophyses (see arrow).

an externally apparent autotomy constriction.

Specimens from north of the Buenos Aires-Tucumán line, have generally brownish color; those from south of this line are generally gray. We are uncertain about the reality of this characteristic as some specimens from the northern portion of the range seem to have a gray cast, but appear brown in places where the surface of the skin has peeled.

Specimens from the southern part of the range have the dorsal portions of their postnuchal annuli narrowed so that the eighth up to the twentieth annuli form posteriorly open angles over the back. This pattern of annulation gives the specimens a "chevroned" appearance (fig. 7). This characteristic angulation is weakly defined in specimens from the province of La Pampa. The equivalent body annuli for specimens from the northern part of the range cross the back at right angles to the long axis of the body.

The relation of tail length to snout-vent length does not show significant differences between specimens from different localities (fig. 8). However,

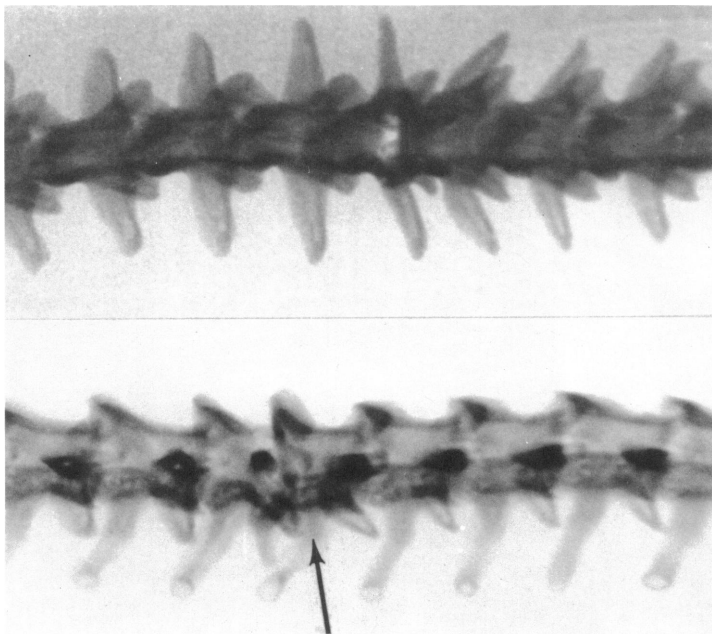


FIG. 6. *Amphisbaena angustifrons plumbea*, dorsal and lateral X-ray view of caudal vertebrae of MHNP 0031, from "Patagonie." Notice vertebral fracture plane and protruding haemapophyses (see arrow).

the relative midbody diameter of specimens from south of the Buenos Aires-Tucumán line is lower (fig. 8) than is that from the more northern specimens. Again, the specimens from La Pampa are intermediate between the other two samples. A histogram of snout-vent lengths suggests that the specimens from south of the Buenos Aires-Tucumán line are shorter, although the samples are rather small (fig. 9).

The smaller specimens from the southern part of the range have a relatively higher and shorter head than the larger ones from the northern regions. The anterior tip of the snout covered by the rostral and nasal shields is relatively broader. However, when comparison is restricted to specimens of equivalent size these differences disappear; consequently they seem to be due to ontogenetic rather than interpopulational differences.

DISCUSSION

Those samples of the present assembly collected north of the Buenos

Aires-Tucumán line, appear to have been taken at localities below 200 m. in altitude. The sample from the provinces of La Pampa and Chubut comes from similar low altitude localities. The specimens from the provinces of Mendoza and Neuquén come from altitudes up to 1000 m.

The northern specimens from Catamarca, Tucumán, Salta, and Chaco, in Argentina, and Tarija in Bolivia, come from localities situated in the proximity of headwaters of rivers, river valleys, or along the edges of

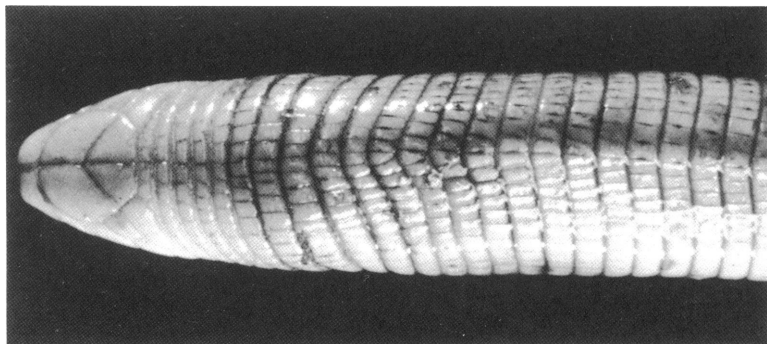


FIG. 7. *Amphisbaena angustifrons plumbea*, dorsal view of head and neck of MCZ 15914, from Mendoza, Mendoza, to show "chevron" or "herringbone" pattern of postnuchal annuli. The sutures have been stained to emphasize pattern.

lowlands and swampy areas. In the southern range, the localities of collection are near the tributaries of the Negro and Colorado rivers, in Mendoza and Neuquén. The specimens from Chubut come from a locality near the seashore, situated in a system of lowlands extending into the provinces of Buenos Aires and La Pampa. The specimens from the provinces of Córdoba and Santa Fé also come from lowland localities. A corridor of similar terrain connects the localities of the northern samples with those from the province of Buenos Aires.

The old record of a specimen from Montevideo, Uruguay, may result from mislabeling, since intensive collecting by M. Klappenbach and his colleagues has not turned up additional specimens of this species.

The northern and southwestern portions of the range are separated by mountain areas with dry climate. These are regions of seasonally flowing rivers, salt flats, and other harsh conditions that may exceed the tolerance of amphisbaenids.

The range of the present assembly seems to be limited by the moisture

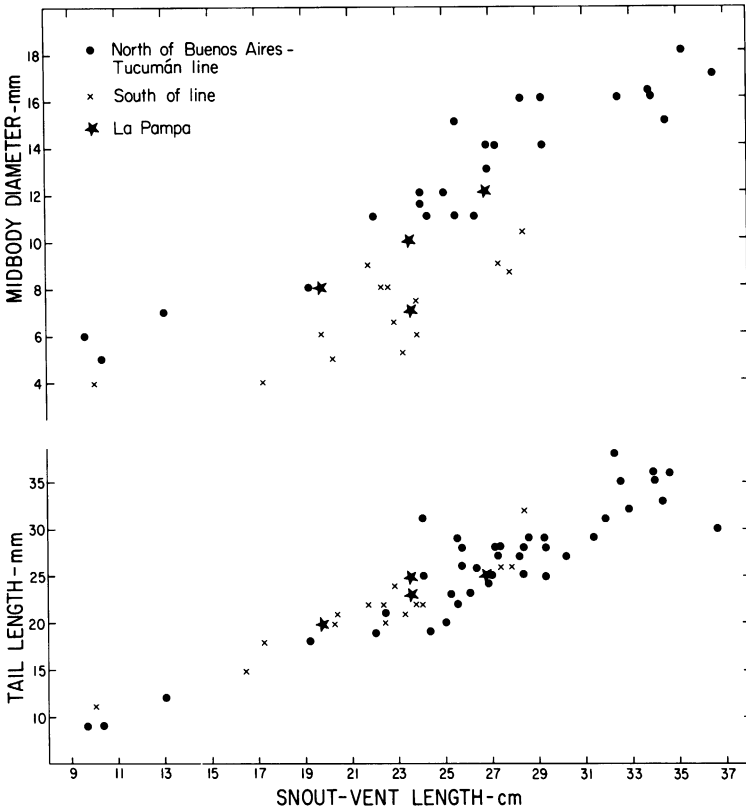


FIG. 8. *Amphisbaena*, scatter diagram of tail length versus snout-vent length (bottom) and plot of midbody diameter versus snout-vent length (top). Data for specimens cited by Gans (1965) are included here.

content and physical characteristics of the soil which amphisbaenids are able to colonize. Such conditions seem to occur along river valleys (Gans, 1968), as well as in the moist lowlands of the Paraná River basin. It is interesting that the present assembly comes from localities spread over the range of more than 1000 km., but which could be connected through ecological corridors along rivers.

The characteristics of the specimens from the extremes of the range, suggest that we are dealing with two distinct species. The characteristics of the specimens from La Pampa are generally intermediate between those of the northern and southwestern samples, suggesting that gene flow occurs between the two populations. We consequently treat the present

assembly as a single species with two well-defined races. The samples from La Pampa and Buenos Aires, furthermore, show geographical proximity. Such sites as La Primavera, La Pampa, and Bonifacio, Buenos Aires, are less than 300 km. apart and very similar topographically. Loventuel is about 100 km. farther west into La Pampa but lies in higher terrain, the

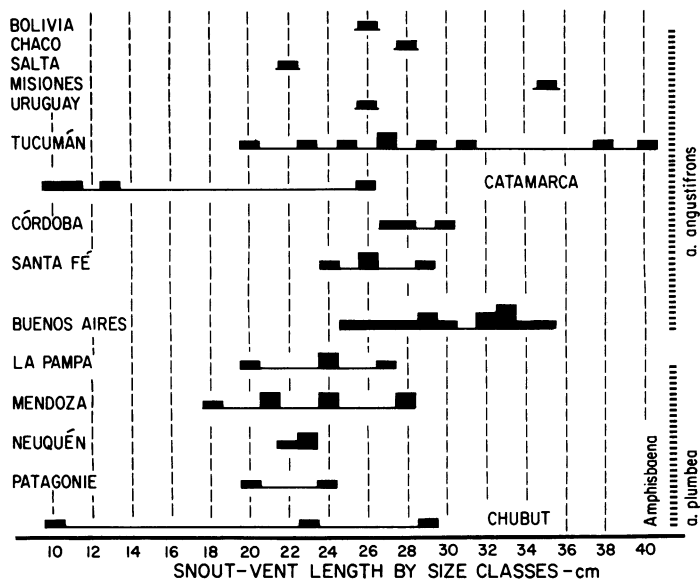


FIG. 9. *Amphisbaena*, histogram of snout-vent length. Data for specimens cited by Gans (1965) are included here.

region ranging from 200 to 500 m. in altitude. The La Pampa region then represents a corridor connecting the two areas.

Additional specimens from along the Negro and Colorado rivers might clarify the present distribution of specimens, as well as variation in characteristics.

Amphisbaena angustifrons

DIAGNOSIS: A medium-to large-sized species of *Amphisbaena* (up to 420 mm. snout-vent length cf. fig. 8), without major fusions of the head shields. Head terminating in a narrow horizontal edge more or less acutely pointed. Generally more than 46 segments to a midbody annulus; body annuli ranging from 205 to 282. Caudal autotomy present or lacking. When autotomy occurs it is at the fifth to ninth annulus. Some specimens

without externally evident caudal constriction, show a vertebral autotomy plane.

Amphisbaena angustifrons angustifrons

Amphisbaena angustifrons COPE, 1861, p. 76 (terra typica: "Buenos Ayres," Argentina; holotype: ANSP 9690).

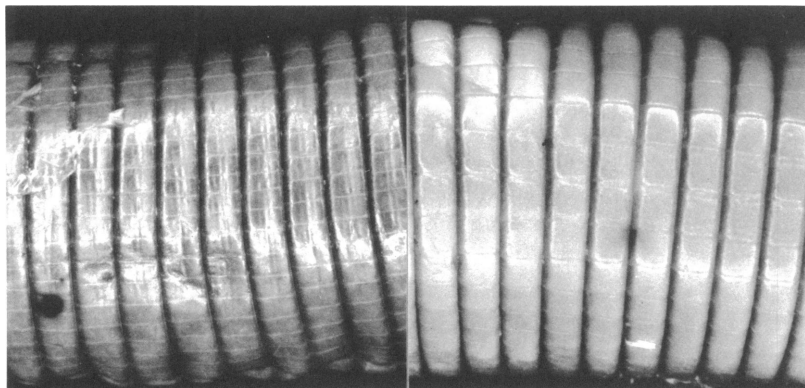


FIG. 10. *Amphisbaena angustifrons plumbea*, dorsal (left) and ventral (right) view at midbody of IBM 0134R from El Sauce, Mendoza, to show pigmentation and segment proportions.

Amphisbaena knighti PARKER, 1928, p. 383 (terra typica: "Bonifacio," Argentina [approx. 36° 18' W]; holotype; BM 1928.5.2.1:RR1946.8.31.76; paratypes: BM 1927.5.26.4 [Bonifacio]; BM 1909.11.2.8:RR1946.8.8.71-1909.11.2.9:RR 1946.8.8.72 [Ajo, Prov. Buenos Aires]; BM 1902.7.29.65 [Tucumán]).

DIAGNOSIS: A large-sized form of *Amphisbaena* characterized by an acutely pointed head terminating in a narrow spatulate tip. The body annuli in the postnuchal region cross the back at right angles. Generally there are more than 48 segments to a midbody annulus and generally less than 205, never more than 218 body annuli. Specimens have a stout body (see fig. 8) and lack caudal autotomy.

DESCRIPTION: See Gans, 1965.

LOCALITY RECORDS¹: URUGUAY: "Montevideo."

ARGENTINA: —. Misiones: —. Buenos Aires: Buenos Aires, AMNH 17023,

¹ This list amplifies but does not repeat that in Gans (1965, p. 21–22) which should be referred to for museum numbers and literature citations. Only specimens newly examined and X-rayed for the present study are listed by number.

65190; ANSP 9690. Vicinity of Buenos Aires. Ajo. Bonifacio. *Entre Rios*: —. Santa Fé: Santa Fé (*ex* La Plata). Bañados del Rincon. Rosário, ZSM 43/1918 (2 specimens). *Córdoba*: —. Córdoba. La Laguna. *Catamarca*: Andalagalá. Esquina Grande. *Tucumán*: Tucumán, CG 3568, 4948, 4949. Ciudadela. Villa Padre Monti, Burruyacú. Valle del Rio Cochuna, El Petrerillo. *Chaco*: —. *Salta*: Urundel.

BOLIVIA: *Tarija*: Upper Pilcomayo, near Villa Montez.

Amphisbaena angustifrons plumbea

Amphisbaena plumbea GRAY, 1872. p. 36 (terra typica: "Mendoza," Argentina; holotype: BM 71.11.29.5-RR1946.8.2.7).

DIAGNOSIS: A medium-sized form of *Amphisbaena* characterized by a seemingly short head terminating in a narrow horizontal edge. The lateral half-annuli of the nuchal region typically meet at a posteriorly open angle presenting a "herringbone" pattern. Generally there are more than 46 segments to a midbody annulus; generally 233–282 (specimens from La Pampa have as few as 210) body annuli. Specimens have a slender body (see fig. 8) and show caudal autotomy between the fifth and ninth caudal annulus.

DESCRIPTION: Meristic characters are summarized in table 1. Figure 13 shows views of the head, figure 14 the ventral surface of the tail, figure 10 segment proportions as well as pattern details.

This is a medium-sized form of *Amphisbaena*. In preservative the specimens are colored a uniform dark gray dorsally, with shades of brown toward the posterior half of the body; some preserved specimens are bleached. Countershading occurs by fading out the pigment along the edges of the segments and complete pigment drop-out on whole segments. In the posterior half of the body the ventral segments may have a narrow line of pigment along the anterior edge, giving the ventrum a striped pattern; the subcaudal surface is generally darker than the ventral surface anterior to the vent. The rostral and prefrontals may be darker than the other head shields.

The head shields show no major fusions. The prefrontals are by far the largest segments on the head, and are in broad contact with the nasals, the second supralabials, the frontals, and the oculars. The angle of the suture between the prefrontals and the frontals varies from nearly 90 to 45 degrees; this suture may be curved. The general pattern of the dorsal sutures of the head is such as to make a posteriorly open angle. The oculars are pentagonal in shape, contacting the prefrontals, frontals, second and third supralabials, and middorsal segments of the first body annulus, generally in line contact. There are three-and-one-half to four, generally four,

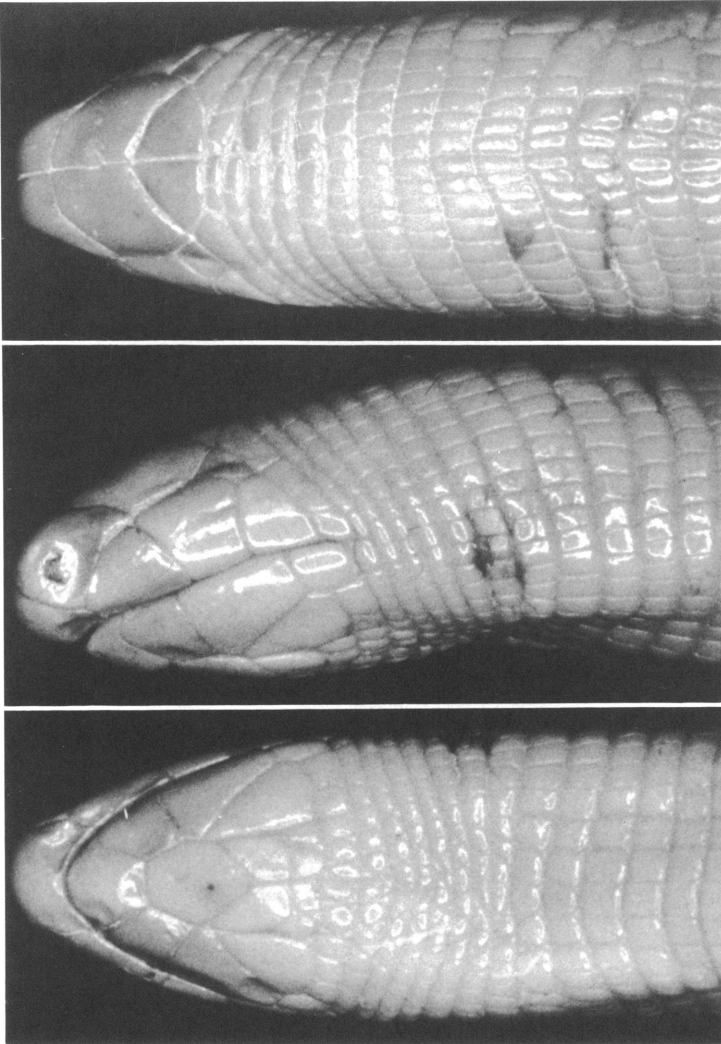


FIG. 11. *Amphisbaena angustifrons plumbea*, dorsal, lateral, and ventral views of the head of USNM 52971, from Mendoza, Mendoza, to show scale proportions.

supralabials; the second is the largest, the fourth is the smallest and the first and third are the same size.

The lower jaw is inserted deeply in the prognathous snout; there are three infralabials, the second being the largest. There is a long contact

between mental and postmental shields. The relative size of these two shields varies: the postmental may be greater, equal, or smaller than the mental. The malars are subtriangular, with a broad contact with the second infralabials. They are generally kept separated from the postmental by the first postgenial. When malars and postmental do contact, it is at a point. The contact region of the malar with the third infralabial may be wide or very narrow. There are one or two rows of postgenials.

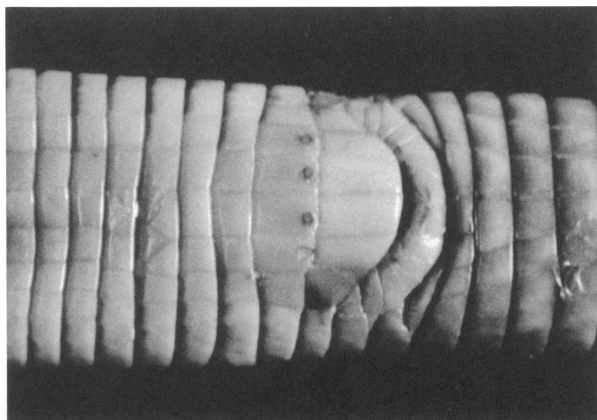


FIG. 12. *Amphisbaena angustifrons plumbea*, ventral view of cloaca of MHNP 0031, from "Patagonie." Notice the clearly demarked precloacal pores.

Shape, number, and spatial relations of these segments show considerable individual variation. The median segments of the second row may insert between those of the first row to contact the postmental; in some individuals the middle shields of the postmalar row send processes between the postgenials, sometimes contacting the postmental. Generally there are two segments in the first postgenial row, five segments in the second postgenial row, and eight to 13 postmalars. The head is slightly narrower than the trunk and the bulging of the temporal muscles quite apparent in large specimens.

In the postnuchal area, beginning at about the eighth body annulus the dorsal segments are shorter than the lateral ones. Consequently the annuli tilt toward the front in lateral view forming in dorsal view a posteriorly open angle which in some specimens may extend as far as the twentieth body annulus. This "chevroned" or "herringbone" pattern can be best seen in small and juvenile individuals.

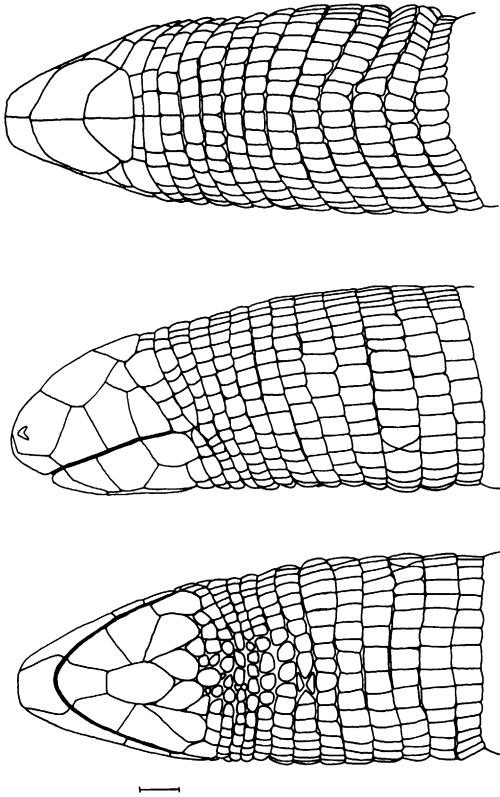


FIG. 13. *Amphisbaena angustifrons plumbea*, dorsal, lateral, and ventral views of the head of BM 71.11.29.5-RR1946.8.2.7, from Mendoza, Mendoza. The line equals 1 mm. to scale. Drawn by J. A. Cochrane.

There are generally four, very pronounced, round precloacal pores. The cloacal segmentation is made of six to nine precloacal and 12 to 16 postcloacal segments. Three to six, normally five, lateral half-annuli correspond to the cloacal area dorsally.

There are 210 to 282 body annuli, from the first segment after the angulus oris up to and including the pore-bearing precloacal. There are 18 to 27 dorsal and 20 to 30 ventral segments to a midbody annulus. The tail bears 16 to 21 caudal annuli before an oval end covered with irregular segments. The tail is rather long and slender in small individuals. Autotomy occurs at the fifth to ninth annuli. The narrowing may not be very apparent, but X-ray analysis invariably shows a vertebral fracture plane.

The lateral sulci appear clearly after the first quarter of the body.

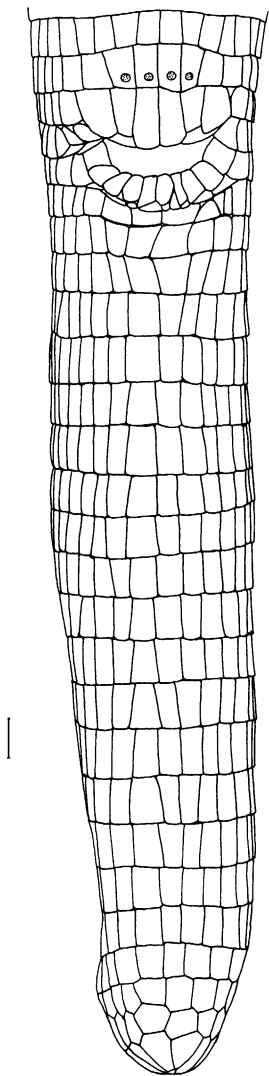


FIG. 14. *Amphisbaena angustifrons plumbea*, ventral view of tail of BM 71.11.29.5-RR1946.8.2.7, from Mendoza, Mendoza. The line equals 1 mm. to scale. Drawn by J. A. Cochrane.

The segments along the ventral side of the body are square along the ventral midline, but become progressively more rectangular toward the lateral sulci. The dorsal segments vary from 1.5 to twice as long as wide.

Alignment of dorsal and ventral sutures of the segments faintly indicates a dorsal as well as a ventral sulcus.

LOCALITY RECORDS: No data: RMNH unnumbered.

ARGENTINA: *Chubut*: Camarones: NMB 6268–6270. “Patagonie”: MHNP 0031–0032. *La Pampa*: La Primavera: MACN 7916–7918 (Gans, 1965). Loventuel: MACN 7196. *Mendoza*: Mendoza: BM 71.11.29.5–RR1946.8.2.7 (Gray, 1872, 1873; Boulenger, 1885; Parker, 1928; Gans, 1967a); MACN 17878 (Gans, 1965); MCZ 15914; USNM 52971 (Burt and Burt, 1930; Liebermann, 1939). El Sauce (just east of Mendoza): IBM 0134–R. Lujan de Cuyo: IBM 0180–R. Capdeville (near Mendoza): SC unnumbered. *Neuquén*: Piedra del Aquila: NMW 8. Auca Mahuida: MACN 7976 (Gans, 1965). Plothier: MACN 10262 (Gans, 1965).

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