

STUDIES ON AMPHISBAENIANS
(AMPHISBAENIA, REPTILIA)

4. A REVIEW OF THE AMPHISBAENID GENUS
LEPOSTERNON

CARL GANS

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 144 : ARTICLE 6 NEW YORK : 1971

STUDIES ON AMPHISBAENIANS
(AMPHISBAENIA, REPTILIA)



4. *A REVIEW OF THE AMPHISBAENID GENUS LEPOSTERNON*

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 144 : ARTICLE 6

NEW YORK : 1971

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 144, article 6, pages 379–464, figures 1–55, tables 1–6

Issued June 28, 1971

Price \$3.25 a copy

This Article completes Volume 144

CONTENTS

INTRODUCTION	383
DISCUSSION OF CHARACTERS	385
General	385
Characters	385
Head Segmentation	385
Annuli	386
Vertebral Numbers	387
Segments	388
Coloration	388
Body Proportions	388
DIAGNOSIS OF THE GENUS	390
THE NON-DIMENSIONAL SPECIES	391
General	391
The situation in Rio de Janeiro	391
The situation in Santa Catarina	392
The situation in Sao Paulo and Parana	393
The situation in Rio Grande do Sul	393
The situation in Paraguay	393
The situation in Bolivia	395
The situation in Argentina	396
The situation in Mato Grosso and Goiás	396
The situation in Minas Gerais and Espirito Santo	397
The situation in Bahia	398
The situation in Pernambuco and Rio Grande do Norte	400
The situation in Pará and Amazonas	400
Summary	401
RECOGNITION OF SPECIES IN SPACE	402
Method of Approach	402
<i>Leposternon scutigerum</i>	402
Selection and Source	402
Variation	402
<i>Leposternon polystegum</i>	406
Selection and Source	406
Variation	406
<i>Leposternon wuchereri</i>	409
Selection and Source	409
Variation	409
<i>Leposternon infraorbitale</i>	409

Selection and Source	409
Variation	410
Separation from <i>L. microcephalum</i>	411
<i>Leposternon microcephalum</i>	415
Selection and Source	415
Variation	415
Summary of variation	433
<i>Leposternon octostegum</i>	435
Supplementary characters	436
Summary and discussion	439
Key to the species	441
TAXONOMIC SECTION	445
Genus <i>Leposternon</i> Wagler	445
Attribution of names	445
ACCOUNTS OF THE SPECIES	451
<i>Leposternon infraorbitale</i>	451
<i>Leposternon microcephalum</i>	451
<i>Leposternon octostegum</i>	456
<i>Leposternon polystegum</i>	457
<i>Leposternon scutigerum</i>	457
<i>Leposternon wuchereri</i>	457
<i>Leposternon species</i>	457
<i>Leposternon incertae sedis</i>	457
SUGGESTIONS TO FUTURE WORKERS	459
Summary	459
LITERATURE CITED	459

INTRODUCTION

THE TAXONOMY of the wide-ranging South American genus *Amphisbaena* has recently been reviewed (cf. Gans, 1967, for citations). This genus is broadly sympatric with the genus *Leposternon*, and it had been observed that the two genera replace each other in various ecological zones (cf. Vanzolini, 1955; Gans, 1966). Hence, it seemed appropriate to compare their distribution patterns.

Still, the genus *Leposternon* represents the last major lacuna in our knowledge of amphisbaenian species. More than 24 forms have been named. At the time the present study was started most were still known from the type alone, and the genus had not previously been reviewed, nor had any of the types been re-described. The absence of review was particularly unfortunate as a cursory survey had confirmed Strauch's comment (1881, col. 93) that certain forms of *Leposternon* showed unusual intra-specific variation in aspects of head scalation and meristic characters, variation far greater than that observed in other South American amphisbaenians.

A review is attempted here. The material is sufficient only to characterize the species pattern in a first-level analysis, to comment on the most interesting variability of characters, and to discuss the status of the types, of which all but one have been reexamined. The present review, as were the previous papers of this series, is intended as a progress report and is designed to facilitate further studies, particularly of amphisbaenian ecology and behavior.

Much of the material reported on herein is old, and a number of the specimens are from collections whose samples are known to have been subject to some confusion. Analysis and presentation of their data are only a first step toward an understanding of the taxonomy of these animals. Subsequent analysis will obviously have to proceed on the basis of fresh specimens, but it is hoped that a statement of information now available may provide a guide for selecting regions most likely to permit fruitful study. In order to facilitate this, and to permit subsequent workers the opportunity of identifying the inevitable errors in this presentation, I have tabulated the information in a standard

format and am depositing all the raw data as indicated under Discussion of Characters.

The present paper is based on specimens from the following museums, identified by the abbreviations given. I am grateful to the curators listed for many courtesies. The collection of the Departamento de Zoologia, Sao Paulo, Brazil (D.Z.) was briefly surveyed during 1963. However, as I could not borrow their *Leposternon* collection that material will have to be reported on at some future time.

- 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 (J. Böhlke and E. V. Malnate)
- A.Z.M., Zoologisch Museum, Amsterdam, Netherlands (D. Hillenius)
- B.M., British Museum (Natural History), London, England (J. C. Battersby and A. G. C. Grandison)
- B.U.M., Zoological Museum, University of Bergen, Norway (H. Kauri)
- C.A.S., the California Academy of Sciences, San Francisco, California (A. E. Leviton)
- C.A.S.-S.U., California Academy of Sciences, Stanford University Collection, San Francisco, California (A. E. Leviton)
- C.G., Carl Gans Collection, Buffalo, New York
- C.M., Carnegie Museum, Pittsburgh, Pennsylvania (N. D. Richmond and C. J. McCoy Jr.)
- D.Z., Departamento de Zoologia, Sao Paulo, Brazil (specimens not examined)
- F.M.N.H., Field Museum of Natural History, Chicago, Illinois (R. F. Inger and H. Marx)
- G.U.M., Zoologisches Institut und Museum der Universität, Göttingen, Germany (P. Kuenzer)
- H.M., Zoologisches Museum, Hamburg, Germany (W. Ladiges)
- I.M.L., Instituto Miguel Lillo, San Miguel de Tucumán, Argentina (K. Hayward and R. F. Laurent)
- I.M.Z.U.T., Istituto e Museo di Zoologia della Università 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)
- K.U., University of Kansas Museum of Natural History, Lawrence, Kansas (W. Duellman)
- M.A.C.N., Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (J. Cranwell and J. M. Gallardo)

- M.C.Z., Museum of Comparative Zoology, Cambridge, Massachusetts (E. E. Williams)
- M.G., Museum de Genève, Switzerland (V. Aellen)
- M.H.N.P., Museum National d'Histoire Naturelle, Paris, France (J. Guibé)
- M.L.U., Martin-Luther-Universität, Halle-Wittenberg, Germany (R. Piechocki)
- 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.P.E.G., Museo Paraense Emilio Goeldi, Belem, Pará, Brazil (D. Albuquerque, O. R. da Cunha, and F. C. Novães)
- M.S.N.G., Museo Civico di Storia Naturale "Giuseppe Doria," Genoa, Italy (E. Tortonese and L. O. Capocaccia)
- N.H.M.B., Naturhistorisches Museum, Bern, Switzerland (H. Sagesser)
- N.H.M.G., Naturhistoriska Museet, Göteborg, Sweden (B. Hubendick and S. Swärd)
- N.M.B., Naturhistorisches Museum, Basel, Switzerland (L. Forcart)
- N.M.W., Naturhistorisches Museum zu Wien, Austria (J. Eiselt)
- N.R.M., Naturhistoriska Riksmuseum, Stockholm, Sweden (U. Bergström and A. H. Westergaard)
- P.U.M., Università di Pisa, Italy (M. Benazzi)
- R.M.N.H., Rijksmuseum voor Natuurlijke Historie, Leiden, Netherlands (M. Boeseman and R. Hoogmoed)
- 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, Michigan (C. F. Walker)
- U.S.N.M., United States National Museum, Smithsonian Institution, Washington, D.C. (D. Cochran and J. A. Peters)
- Z.I.L., Zoological Institute, U.S.S.R., Academy of Sciences, Leningrad, U.S.S.R. (I. 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). [Specimens marked * arrived too late to be included in the data analysis.]

Once again I would like to express my gratitude to the colleagues who have assisted me by providing geographical information, in particular to Mr. W. C. A. Bokermann. I am also grateful to Drs. H. G. Dowling and I. Gilboa of the Herpetological Information and Search Systems. Mr. C. O. Diefenbach helped by checking locality names. A number of people participated in this project, both in determining and checking the counts and in formulation of the hypotheses. Among these are Mr. K. James Clark, Mr. Paul Tenser, Mr. Mark Amdur, Mrs. A. S. Gaunt, Mrs. Jane Bell, and Miss Susan Wade. I am grateful to my colleague, Dr. A. K. Bruce, for permission to use his X-ray facilities. Dr. Virginia Cummings provided the drawings.

It is a pleasure to acknowledge that this protracted study has been supported by National Science Foundation Grants Nos. GB 2460 and GB 6521X.

DISCUSSION OF CHARACTERS

GENERAL

THE SEGMENTATION PATTERN of *Leposternon* differs markedly from that shown in the species of *Amphisbaena*. Consequently, it is necessary to use a slightly different system of counting and description from that most recently detailed by Gans (1966), but the pattern of data presentation follows Gans (1966). For data of tabulated characters, order NAPS Document Number 01385 from ASIS National Auxiliary Publications Service, c/o CCM Information Services, Inc., 22 West 34 Street, New York, New York 10001. Advance payment is required. To order, cite Document number and remit check or money order payable to ASIS NAPS—\$2.00 for microfiche, or \$7.00 for photocopies. Data for these specimens can be obtained (on microfilm aperture card) from: Herpetological Information Search Systems, the American Museum of Natural History, New York, N.Y. 10024. The order of specimens in the appendix is that under "Distribution records." Whenever possible the spelling of locality names has been standardized according to the Index to map of Hispanic America 1:1,000,000 (Hanson, 1945).

CHARACTERS

HEAD SEGMENTATION

The anterior tip of the head is pointed and roundly spatulate. The edge of the spade passes from the rostral keel laterally, parallel with the lip, terminating just ventral and somewhat posterior to the eye. The gular fold passes immediately posterior to the cephalic shields; it extends up the sides of the head and is characterized by a number of narrowed body annuli separated by wide areas of unscaled skin.

The dorsal surface of the head rises smoothly in a straight line or concave curve. It is covered with more or less enlarged segments. The rostronasal and one (or more) of the following segments are always azygous, although a pair of median enlarged segments (prefrontals) may intervene between them. The ventral surface of the head is more or less flattened, and the edge of the jaw is strongly countersunk. The infra-

labial and postmental segments protrude and are relatively large.

The rostronasal and part of the following segments on the dorsal surface of the head may be keratinized in some forms, particularly in larger specimens. In other populations these segments are distinctly non-keratinized or even underlain by a loose layer of connective tissues which deforms in preservatives. The deformation induces a remarkable folding of the rostral surface that masks and imitates the outlines of the cephalic segments and complicates the description of the head segmentation.

Any group of species showing fusion of cephalic shields incorporates the seeds of nomenclatural confusion. In "homologizing" segments one must differentiate between segments that fuse or subdivide, in which case the over-all spatial proportions are maintained, and those that shrink or expand, leading to a shift in the regions they occupy. The first situation is seen in the rostronasal fusions and the second in the caudad displacement of the posterior frontal edges in certain forms. In other instances, such as the prefrontal subdivisions, we are unable to determine by what steps the observed patterns were produced. The present material does permit certain conclusions regarding presumptive homologies.

1. There is invariably a large azygous shield that forms the medial portion of the anterior lip. The nostrils are inserted into this segment suggesting that it represents a fused rostronasal.

2. Most species have a large first supralabial followed by much smaller segments near the angulus oris. Two of the forms, *L. infraorbitale* and *L. polystegum*, show a small supralabial anterior to this. When the separate segment is found, the share of the rostronasal of the labial edge is reduced, suggesting that these are first supralabials which in other forms are fused to the rostronasals. Whereas the second supralabial of some species may thus be considered homologous to the first supralabial of others, the use of such terminology leads to confusion in routine descriptions. The supralabials for each species are hence numbered only when they are discrete.

3. The nomenclature of the enlarged segments on the dorsal surface of the head poses far greater problems. The posteriormost of the two more or less

enlarged and azygous medial head shields was referred to as a frontal by Strauch (1881, column 93) and accepted as such by various subsequent authors. Yet, this segment lies medial to the eyes, and at least in part, anterior to a line joining the posterior aspects of the oculars; this line has been used to define the limit of the very large prefrontals in the genus *Amphisbaena* and similar forms (Gans and Alexander, 1962, fig. 5). Strauch's frontal, rather, corresponds to the variable-sized, azygous shields that are occasionally noted at the intersection of the midsagittal suture and that may lie between prefrontals and nasals (cf. Brongersma, 1932). In order to avoid confusing homologies, the enlarged median shield is hereafter referred to as the azygous, and the shields immediately flanking it as supraoculars. Most specimens of *L. infraorbitale* also have a small infraocular ventral to the ocular and above the posteriormost, small supralabial.

The term prefrontals is retained for the segments anterior to the azygous and the supraoculars, but it must be recognized that they are only partially homologous to the prefrontals of *Amphisbaena* and similar forms. Their size varies with the size of the azygous, which they may exclude from contact with the rostronasal, and in some forms, they fuse with the supraoculars or the azygous.

4. The paired, enlarged median segments immediately posterior to the azygous are then the frontals, to which a slightly enlarged pair of parietals may be fused. A variable number of segments is also found in the temporal region. It appears as if the variability of this region is again very large, and it is suggested that the variability results from the overlap of the functional influence extending caudad from the snout and that extending anteriorly from the body (and indeed from the pectoral region).

5. When seen in ventral view, most species show a mental that may be fused to the postmental (genial). In most forms mental and postmental extend posteriorly to the edge of the organized segments of the lower jaw, that is, they reach the edge of the gular fold. A few postgenials are very rarely separated off here.

6. There is invariably a very large infralabial segment corresponding in extent along the labial edge to the large supralabial opposite which it lies. A few forms have discrete, small first infralabials, but these, in most cases, appear to be fused to the enlarged second infralabials.

7. Several pairs of slightly enlarged segments may occur in a malar region, intercalated between the posterior edge of the postmental (genial) and the medial edge of the small, second infralabials. Another more anterior pair of "malar" segments may be intercalated between postmalar and first infralabial. In one population these segments and some of the smaller ones flanking them are fused into a single segment with the enlarged infralabial.

ANNULI

The annulation pattern of a large number of specimens proved to be far more irregular than in the genus *Amphisbaena*. Rather than representing a series of annuli or half-annuli ending more or less squarely at the lateral sulci, the ends of many of these terminate in wedge-shaped areas that intercalate, singly or in groups of up to five, between two annuli of the adjacent quadrant. In a few forms all these wedges terminate across lateral bands that in the living animals apparently line the lateral sulci. These sulci then involve not only two or three rows, but up to 10 rows of adjacent segments. In other forms many annuli continue across the sulci to terminate in the center of one of the quadrants. In certain specimens the pattern is so irregular that the concept of annuli, implying slices of a right circular cylinder, is no longer truly descriptive. The rows of segments pass along the periphery of the cylinder for angular distances not corresponding to multiples of 90 degrees.

This situation became immediately apparent when the first annulus counts were repeated. Only when counts were made along a fixed line (initially the tenth to the fifteenth segment ventral to the left sulcus) were they reproducible (99% of counts within ± 2 annuli). Each of the four quadrants was counted separately on a large series of specimens. Left and right counts did not show any major differences, but the dorsal counts of certain populations were significantly higher than the ventral counts. The tables thus list longitudinal counts of postpectoral annuli, made both dorsally and ventrally.

Even though both dorsal and ventral counts of postpectoral annuli were recorded and compared, it is of interest to ask whether either of these parameters might be determined directly and whether the other thus represents a variant thereof. The large and fairly well-preserved samples from Joinville appear ideal for this comparison. The population estimate of the standard deviation, s , was 5.72 for dorsal ($N=119$) and 2.71 for ventral ($N=122$) counts, whereas the coefficient of kurtosis was -1.96 for the former and -1.35 for the latter. These results suggest that the dorsal count is more variable and that it is appropriate to discuss the addition of dorsal half-annuli rather than the dropping out of accessory ventral ones.

The extra dorsal "half-annuli" are not randomly distributed along the length of the

animal. The tables thus list the difference between dorsal and ventral annuli, expressed as dorsals minus ventrals, for each unit of 50 ventrals proceeding caudad. The series $5+6+8+9+11$ then means that counts of 55, 56, 58, 59, and 61 were obtained respectively for the first, second, third, fourth, and fifth group along the dorsal surface. Extra half-annuli caudad to the 200th ventral are included in the last figure, so that the total number of ventrals is 270 and of dorsals, 309 for this specimen. Both dorsal and ventral counts are apparently significantly higher than twice the number of vertebrae (cf. Alexander and Gans, 1966, but note that these authors listed body, rather than postpectoral, annuli).

Counts of dermal body annuli were subdivided and recorded for four contiguous, but non-overlapping zones referred to respectively as anterior laterals, postpectoral annuli, laterals, and caudals. The separation of anterior laterals and postpectorals permitted analysis of the number of body annuli involved in pectoral shield formation. The counts reported may be compared with those of "body annuli" published for other amphisbaenian species (Gans, 1966) by adding these two categories.

The position of the angulus oris has previously been used as the indicator of the first body annulus. In *Leposternon* it appeared preferable to start counts of the anterior laterals from the posterior edge of the enlarged head shields. The lateral segments of the first annuli are often hidden in specimens with the heads fixed in a depressed position. This introduces an additional error into the counts. One to two additional half-annuli ordinarily occur between the angulus oris and the first annulus passing back of the enlarged head shields, and the count of anterior laterals should theoretically be increased by this value.

Anterior laterals are those dorsal half-annuli corresponding to the zone of pectoral modification. They are counted from the first annulus (often reduced to two or three segments flanking the middorsal line) posterior to the last of the highly keratinized dorsal head shields and up to and including the annulus immediately anterior to the first postpectoral annulus.

Postpectoral annuli include those from the first one that extends continuously across the ventral surface posterior to the modified pectorals, up to and including the annulus just

anterior to the large precloacal shields. The postpectoral annuli of *Leposternon* are remarkably irregular and the intercalated half-annuli do not start at the lateral sulci, but often begin either dorsal or ventral to these. The sulci are hence both wide and irregular.

Laterals are those half-annuli lying between the last postpectoral annulus and the first caudal.

Caudal annuli are counted from the first complete (ventrally not reduced) postcloacal up to and including the last complete annulus showing regular segments. The last lateral and first caudal often share two large segments flanking the midventral line. The tip of the tail appears as a group of irregularly arranged segments.

VERTEBRAL NUMBERS

The genus *Leposternon* appears to be exceptional in the Amphisbaenia in lacking a regular correlation between the number of vertebrae and that of dermal annuli. The vertebral number is hence considered as a separate parameter. All specimens (except those lacking all data or referred only to "Brazil" or "Argentina") were consequently X-rayed by techniques described in the earlier paper (Alexander and Gans, 1966; Kerfoot, 1970). The number of vertebrae from head joint to sacral region (post axial of Hoffstetter and Gasc, 1969) and the number of "lateral" and caudal vertebrae ("cloacal" and "caudal" of Hoffstetter and Gasc, 1969) were included in the tables of data and used in analysis.

The results of the analysis proved interesting in that the variance of the vertebral number appears to be significantly smaller than that of numbers of anterior lateral plus postpectoral (=body) annuli. Although there are approximately 2.5 dermal annuli to each vertebra, this ratio varies widely and the range of vertebral numbers is remarkably restricted, not only within a given species but also for the genus as a whole; thus the number of vertebrae ranges from 82 to 141, whereas the number of postpectoral annuli ranges from 177 to 378. The ratio of ranges is thus 59/201 and becomes even more significant if the comparison is only for the situation in *L. microcephalum* (23/94).

Further clarification results from analyses of the few individual samples. The two largest are those from Joinville and Humboldt. In each of these the vertebral number appears to approach a somewhat skewed normal distribution without

any secondary peaks; the distribution of numbers of postpectoral annuli seems bimodal or multimodal. This observation again confirms remarks (Gans and Alexander, 1962, p. 76) that multiple components contribute to the observed variability of dermal annuli. No significant differences appeared between the numbers of caudal vertebrae noted for the different species.

SEGMENTS

The segments of an annulus are irregular; their number and relative shape tend to vary drastically between adjacent annuli masking serial and interspecimen differences. A further complication is due to the wedging down rather than blunt termination of the annuli. The centers of the lateral sulci are thus indicated by a raphe between full-sized segments rather than by a wide empty region or one filled with small irregular segments. Counts of dorsal and ventral half-annuli must start and stop at this modified intersegmental raphe; they cannot proceed to the tips of the wedge-shaped endings. If this caution is ignored one obtains not only a total (dorsal plus ventral) count greater than the number of segments around the body, but furthermore increases the already great differences between successive counts.

Dorsal and ventral segments were counted in the midbody region, for an annulus selected at random, and for the four to five annuli adjacent to it; the means of each set are recorded as dorsals plus ventrals (dorsals/ventrals in the raw data). When the values for a specimen are given in parentheses they represent an earlier and presumably less standardized count on a specimen no longer at hand at this writing.

The anterior lateral annuli are only complete on the dorsal and lateral surfaces. Ventrally they adjoin a zone of pectoral modification. The anterior portion of this zone consists of groups of irregularly shaped, reduced, and rounded segments that run into the almost naked gular folds. More posteriorly the pectoral segmentation becomes more regular. The interannular sutures often appear to bend through an 80-degree turn

to form elongate segments parallel to the midline. The largest such shields generally lie along the ventral midline, and one or two pairs of shields on each side of the midline contribute to the pattern mentioned above. Patterns of pectoral segmentation have been recorded when correlated with other characters.

COLORATION

The various specimens are generally pigmented only faintly, and variably countershaded, but no discrete color patterns were noted. Pigmentation is generally countershaded and pigment is restricted primarily to the dorsal and lateral surfaces, although ventral pigmentation of the tail occurs. In some cases the whole body surface is pigmented; in other specimens the pigmentation starts after the first third of the body. Many specimens lack all pigment, and it is then impossible to distinguish pigmentless and faded conditions. Pigmentation may, furthermore, fade selectively. Thus dark centers of segments remain noticeable for several rows below the lateral sulcus and for the posterodorsal aspect of the tail in specimens from Bolivia; but the even ground color of the dorsal surface and the color of the segmental margins generally bleach completely.

A wide range of variation occurs in arrangement and density of pigment on the segments. Segments show two extremes of pigmentation with numerous intermediates. The first extreme is a dark central spot on a light background. The second is a complete and even pigmentation of the segment. Differences consistent for a particular population are mentioned in the text.

BODY PROPORTIONS

Snout-vent and tail length were read by depressing the specimen to a meter stick. Midbody diameter was measured to the nearest millimeter at the widest, undeformed site along the first third of the trunk. When the trunk was elliptical, the mean of the sum of major plus minor axes was recorded.

DIAGNOSIS OF THE GENUS

THE GENUS *Leposternon* as here defined includes specimens with a range in postgular annulus counts from 176 to 372. Vanzolini (1951) characterized the genus as follows:

"Snout pointed. Nasals [skeletal elements] not meeting on the midline and excluded from the rim of the nostrils. Partes posteriores choanarum absent. Dentition 7:5:7. Several large shields on top of head. Pectoral shields highly variable. Preanal [=precloacal] pores absent."

This characterization may be amplified and modified by noting that these are relatively large, stout animals in which the head is always dorsoventrally compressed. The nostrils open on the ventral surface of the snout and a suture connects each to the edge of the mouth. The rostral and nasals are fused into a single shield that is followed by a sequence of one to five enlarged segments along the dorsal surface of the snout. At least one of these (postrostral) shields is always median and azygous. A gular fold lacks

segmental cover. There are significantly more than two dermal annuli per vertebra. All specimens have very short, bluntly rounded tails and lack caudal autotomy; one species (*L. polystegum*) has one (rarely two) faintly expressed precloacal pores on each side.

Included here are all South American amphisbaenians that cannot be assigned to the genera *Amphisbaena*, *Anops*, *Aulura*, *Bronia*, and *Mesobaena*.

The genus *Leposternon* ranges across eastern South America. Its range extends north to the Amazon in Pará, Brazil, inland up the Amazon, thence south through east-coastal and central Brazil to the state of Santa Catarina (and perhaps Rio Grande do Sul), inland to Amazonas, Goiás and Mato Grosso, southwest into Bolivia and Paraguay, and then south into Argentina with records in the Argentine states of Entre Rios, Corrientes, Misiones, Formosa, Chaco, and Salta (figs. 1, 2).

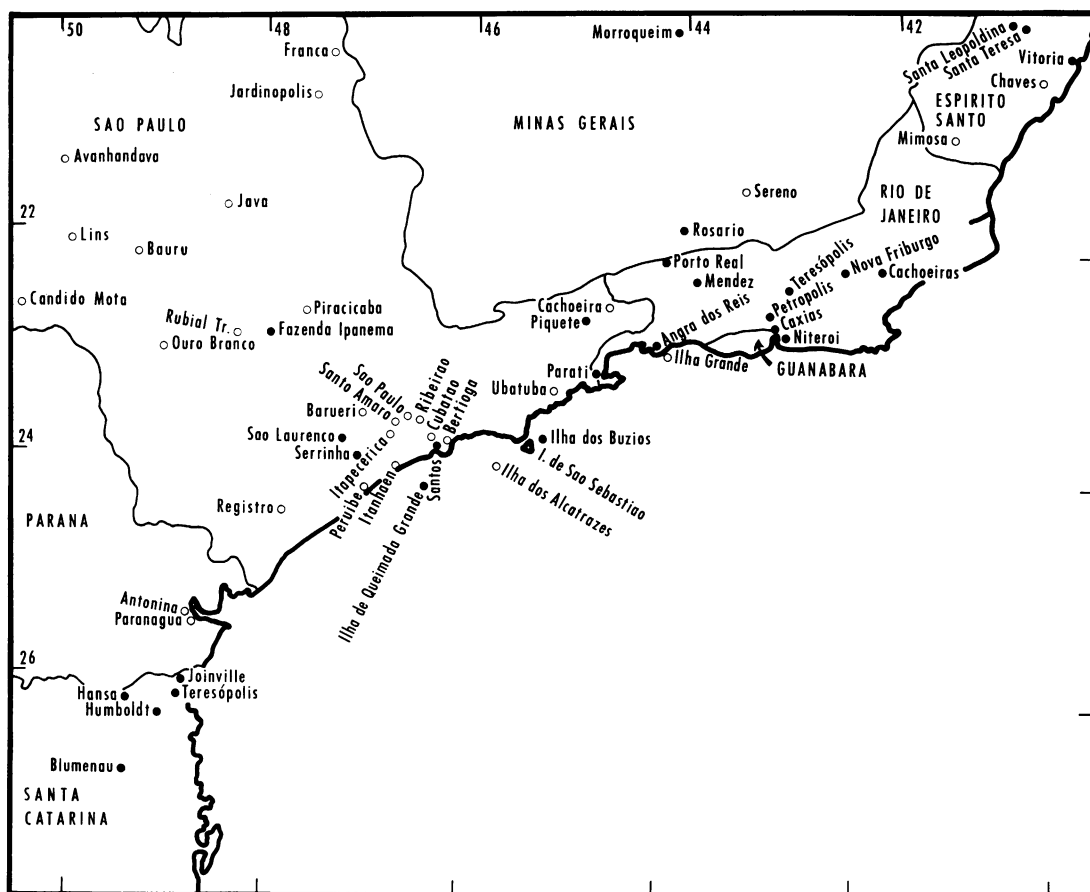


FIG. 2. *Leposternon*. Sketch map of localities in southeastern Brazil.

THE NON-DIMENSIONAL SPECIES

GENERAL

THE PRESENT ANALYSIS generally proceeds by the method of non-dimensional species, outlined in previous papers of these series, most recently in Gans (1966). The greatest source of uncertainty is due to the inadequate size and scattered distribution of the samples. Thus the demonstration of sympatry generally leaves much to be desired. Taxonomic decisions are hence kept conservative and the steps of the analysis documented as clearly as possible to facilitate comparisons as better localized samples become available.

The comparisons of sympatric samples are always started with an analysis of the number of (ventrally counted) postpectoral annuli. The groupings thus defined are compared for other characteristics, of which the pattern of cephalic segments proved to be most useful. Parallel differences in several, presumably non-associated characteristics are assumed to indicate that the groupings represent samples drawn from discrete species.

In order to facilitate future reference to the discussion of non-dimensional species and of geographical variation, the specific names finally assigned have been added in parentheses. This does not imply a prejudgment of the case but is intended to simplify a cross check between these early discussions and the summary statements defining the several species.

The two largest samples come from the vicinity of the city of Rio de Janeiro and from coastal Santa Catarina, Brazil. These are, hence, dealt with first. Following this come comments on the samples available from adjacent regions, proceeding first to the south and west and next to the north.

THE SITUATION IN RIO DE JANEIRO

The 104 specimens from the city and state of Rio de Janeiro, including the state of Guanabara, may be subdivided into an assemblage (seven specimens) with high ($R=255-292$, $m=269$) and another (95 specimens) with low ($R=181-226$, $m=203$) numbers of postpectoral annuli. Two specimens, one with 238, the other with 242 postpectoral annuli, fall between these

counts. The four groupings characterized on the basis of numbers of postpectoral annuli also differ in their head segmentation pattern. Further, less well-defined differences occur in number of vertebrae, snout-vent length, tail length, numbers of anterior laterals, midbody diameter, and the arrangement of pectoral (i.e. anterior ventral) segments. Although there are varying degrees of overlap for the latter characteristics (table 1), they, nevertheless, support the differences noted in postpectoral counts and head segmentation patterns.

The dorsal head pattern of the Rio-low group (*=microcephalum*) is complexly divided into some five rows of shields (figs. 3A, 4A). More than 80 per cent of all specimens in this group show various degrees of vertical folding on the prefrontals, approximately 32 per cent show various degrees of fusion between the azygous and frontal shields, and four specimens have a vertically furrowed azygous shield. The proportions of the head elements are, however, maintained constant regardless of the degree of fusion or furrowing. The posterior cephalic shields are usually darkly pigmented. There are two supralabials; the first of these is by far the largest. The ventral gular fold may be filled with small, rounded segments spaced widely apart on non-segmented skin. The pectoral region also shows a pair of elongated, medial segments. The more lateral rows of slightly elongated or simply enlarged scales slant toward the midline and are disposed in an arrangement of anteriorly open chevrons. The segmental pigmentation on the dorsal and lateral surfaces of most specimens consists of a dark, central spot on a light background; a few specimens also show this coloration on the ventral surface of the tail.

The dorsal head pattern of the Rio-high group (*=scutigerum*) is drastically different. The head is covered by three rows of scales; the anterior two each consist of a single, large, heavily keratinized shield (figs. 3B, 4B). The ventral head scales are also reduced in number. The large central head scale forms a "brow" when viewed laterally. The eyes are displaced laterally and are barely visible in dorsal view. The pectoral region is covered by at least three pairs of elongated, irregularly shaped segments with the

TABLE 1
ANALYSIS OF SYMPATRIC SAMPLES FROM THE STATES OF RIO DE JANEIRO AND GUANABARA

	Group 1 (Low)	Group 2 (High)	Group 3 (M.C.Z. No. 1363)	Group 4 (N.M.W. No. 12372)
No. of Specimens	95	7	1	1
Head Segment Pattern	fig. 3A, 4A	fig. 3B, 4B	fig. 3C, 4C	fig. 3D, 4D
Nos. of Annuli (Anterior Laterals + Postpectorals)	(12-18) + (181-226) (m=203)	(14-17) + (255-292) (m=269)	14 + 238	14 + 242
No. of Body Vertebrae	93-103	119-123	96	118
Snout-Vent Length (in mm.) Minimum-Maximum	122-494	292-457	575	304
Pectoral Pattern	Elongated pair of segments on midline; additional pairs, elongated or enlarged, may slant toward these median segments	3 pairs of greatly enlarged segments; hourglass-shaped pattern	Slightly enlarged segments in rows slanting to indistinct midline	3-4 pairs of elongated segments partially fused with one another

two median pairs placed in a distinct hourglass pattern. Dorsal pigmentation is lacking or indistinct.

The two specimens that do not fit into either the Rio-high or the Rio-low groups differ from each other as well. The one with a count of 236 (= *infraorbitale*) is notable in that it is both longer (snout-vent length) and wider (midbody diameter) than any other specimen in the Rio assemblage. The head pattern (figs. 3C, 4C) of this specimen is generally similar to that of the Rio-low group. The arrangement of dorsal head segments varies in proportion. There are three supralabials, with the first and third much smaller than the second. The specimen is also unique among Rio specimens in possessing an infraocular dorsal to the third supralabial. The pectoral scales are enlarged and relatively rounded, rather than elongate, and arranged in slanting rows that meet to form anteriorly open chevrons at the midline.

The specimen with a count of 242 (= *wucheri*) has a head pattern notable for an enlarged azygous scale (figs. 3D, 4D) that is proportionally broader than that characteristic of the Rio-low group, or of the very large specimen. Further, the azygous sends a narrow tip between the prefrontals to meet the rostronasal. The pectoral pattern consists of three to four pairs of elongate

segments, the ends of which show blindly terminating sutures that suggest that these arose by fusion of smaller elements.

There are definitely two, and probably four, species in the state of Rio de Janeiro.

THE SITUATION IN SANTA CATARINA

The sample (= *microcephalum*) from coastal Santa Catarina (the cities of Hansa, Blumenau, Therezopolis, Joinville, and Humboldt, and the state of Santa Catarina) is the largest available (N=224) but cannot be subdivided on the basis of any meristic datum (postpectoral annuli, R=190-216, m=201). Every character shows an apparently unimodal distribution with only slight variation within the range noted above for the low group of the Rio de Janeiro sample.

In dorsal view the head segments agree with the Rio-low pattern, although there is somewhat more individual variability in the configuration of the azygous. The degree of vertical folding of the prefrontals is in many cases great. The pectoral pattern and head and body coloration resemble that of the Rio-low group.

From this evidence there is no indication that more than a single species occurs in the state of Santa Catarina.

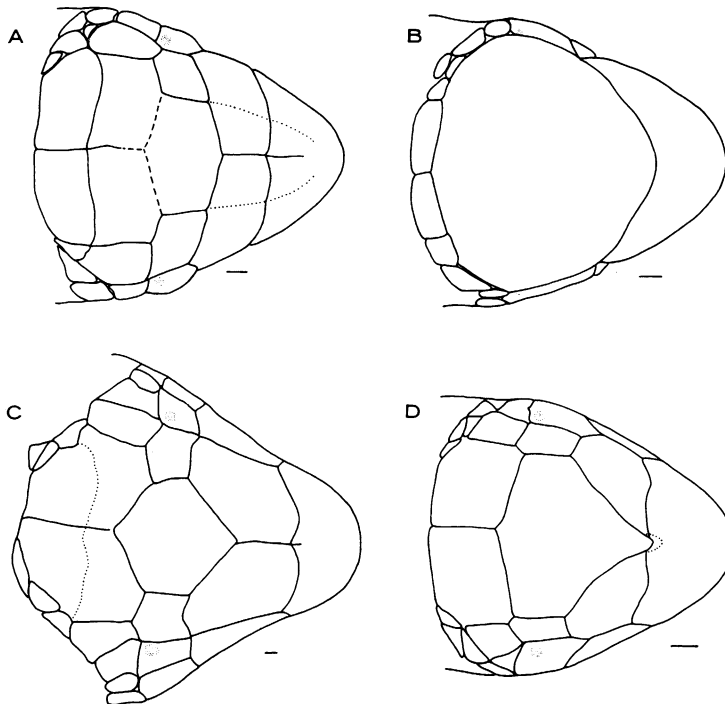


FIG. 3. Four patterns of head scalation in specimens from states of Rio de Janeiro and Guanabara, dorsal views. A. Group 1 (*Leposternon microcephalum*). B. Group 2 (*L. scutigerum*). C. Group 3 (*L. infraorbitale*). D. Group 4 (*L. wuchereri*). Dotted lines indicate areas of folding; dashed lines indicate raphe that are absent in large segments of a population. Lines equal 1 mm. to scale.

THE SITUATION IN SAO PAULO AND PARANA

The sample from the states of Sao Paulo (37 specimens) and Parana (two specimens) represents an assemblage with low ($R=185-238$, $m=205$) numbers of postpectoral annuli. The head segment patterns for all but two Sao Paulo specimens show only minor variations, well within the range noted above for the low group sample of Rio de Janeiro and that from Santa Catarina. The posterodorsal segments of the head are usually darkly pigmented. Body coloration and pectoral pattern resemble that of the Rio-low assemblage.

Two specimens (F.M.N.H. Nos. 69954, 69955) from the vicinity of Fazenda Ipanema, Sao Paulo show additional variation in their head pattern. Here the azygous continues between the prefrontals to the rostronasal, and the azygous is shield-shaped. Ventrally, the medial paired malars are broken into three small seg-

ments, whereas the first infralabials have fused to the lateral pair of malars (fig. 5). The pectoral pattern is similar to that of the Rio-low group except for a more diamond-shaped appearance of the segments. As the meristic characters of these two specimens fall in the center of the range for the remainder of the Sao Paulo material there is no reason to treat them as more than local variants. Hence, only a single species would seem to occur in Sao Paulo and Paraná.

THE SITUATION IN RIO GRANDE DO SUL

One specimen without further locality (*=microcephalum*) is available from the state of Rio Grande do Sul. It has low numbers (199) of postpectoral annuli and is otherwise similar to the specimens from Santa Catarina.

THE SITUATION IN PARAGUAY

The sample from Paraguay (*=microcephalum*)

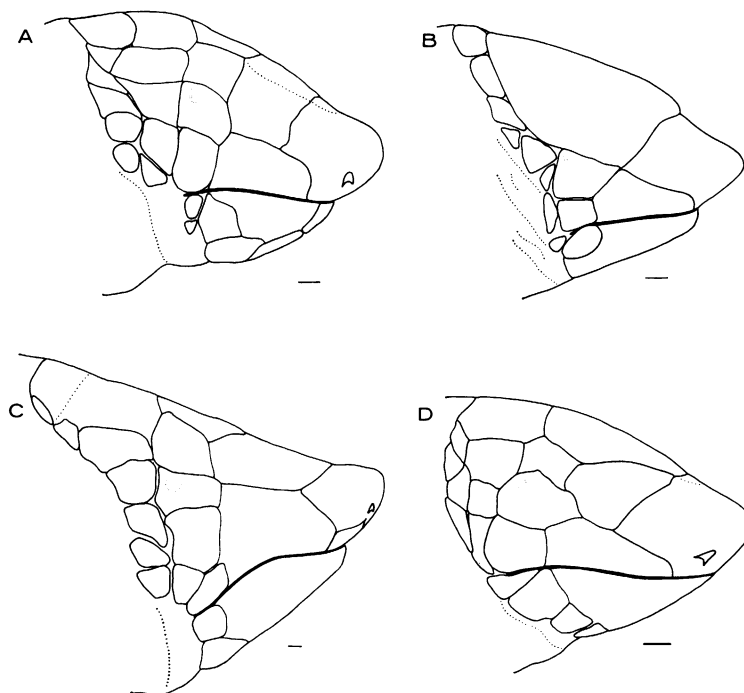


FIG. 4. Four patterns of head scalation in specimens from states of Rio de Janeiro and Guanabara, lateral views. A. Group 1 (*Leposternon microcephalum*). B. Group 2 (*L. scutigerum*). C. Group 3 (*L. infraorbitale*). D. Group 4 (*L. wuchereri*). Dotted lines indicate areas of folding. Lines equal 1 mm. to scale.

consists of 49 specimens (about 15 of these were examined in other collections after completion of this portion of the analysis). It appears to be unimodal on the basis of all meristic characters checked for this study, although the range of postpectoral annuli ($R=200-271$) is relatively greater and the mean ($m=239$) significantly higher than those of such large conspecific samples as that from Santa Catarina. This assemblage poses great difficulty because it includes three obviously distinct patterns of cephalic segmentation (table 2 and fig. 6). (Specimen H.M. No. 3438 labeled "Paraguay" without any other indication seems to belong with specimens from eastern Argentina and is hence omitted here.)

The first group ($N=19$) shows a cephalic pattern similar to that of variant specimens from Sao Paulo (fig. 6A) except for the constant lack of supraoculars (and the lack of any enlargement of the segments of the pectoral region). The azygous tends to be shield-shaped, and in narrow contact with the rostral. Posterior seg-

ments of the head are almost always darkly pigmented as in the samples from Rio-low and Santa Catarina. Members of this group in many cases show the frontals and parietals fused, but they never lack a complete raphe between azygous and frontals.

The second group ($N=6$) has a much wider azygous scale which shows broad contact with the rostronasal (fig. 6B). The posterodorsal head segments do not seem to be pigmented. The first and very large infralabial is in many cases fused with the medially placed, lateral malar.

The third group ($N=9$) shows varying degrees of loss of the raphes between the azygous and prefrontal segments as well as fusion of both infralabials and the lateral pair of malars (fig. 6C). A pair of blind raphes generally extends anteriorly from the posterior edge of this composite segment indicating its nature. The posterior aspect of the head does not appear to be pigmented.

Some specimens are intermediate between these patterns in one or another characteristic,

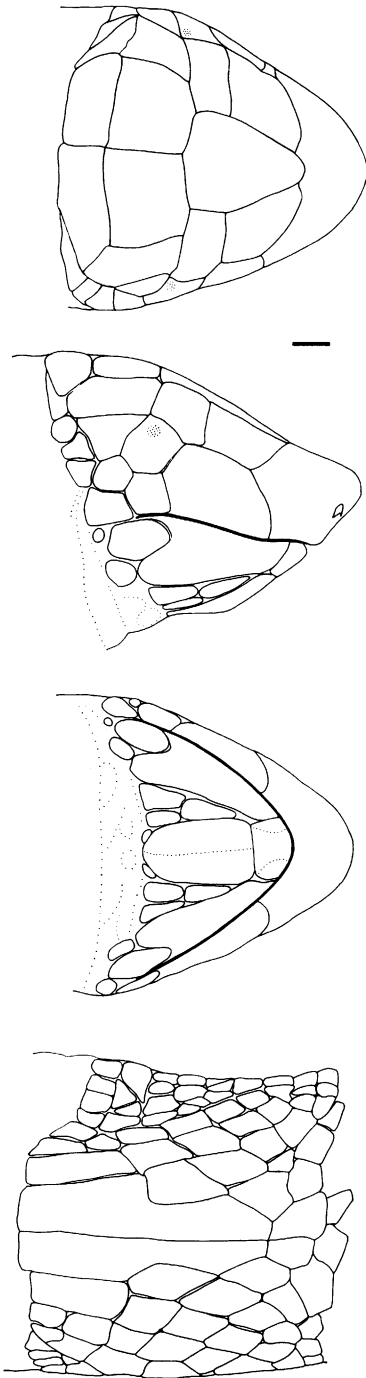


FIG. 5. *Leposternon microcephalum*. Pattern of head scalation. Dorsal, lateral, and ventral views, and pectoral scalation of F.M.N.H. No. 69954, from Fazenda Ipanema, Sao Paulo. Dotted lines indicate folds, not sutures. Line equals 1 mm. to scale.

but such intermediacy is often unilateral and generally applies only to the dorsal or ventral surface. All of these groups agree in lacking the vertical folding of the facial region, noted in samples from Rio-low and Santa Catarina, and also agree in sharing a minimal elongation of pectoral segments; the latter are quite generally enlarged and diamond-shaped.

The segmental pigmentation in all three groups ranges from a dark central spot and light perimeter on each segment to a more or less even segmental pigmentation. When the sample is divided according to the three head patterns, the groupings do not show significant differences in meristic characters or body proportions.

The material from Paraguay is sampled from across a fairly large range and the possibility of internal geographical variation must be considered. A map (fig. 7), including some Argentinian localities, indicates that all localities except Asuncion, show only a single pattern. Generally speaking, the more western localities show the first pattern, and the more eastern localities the second pattern. The very distinct third pattern only occurs at two localities, Asuncion and Colonia Elisa. For the moment then, it seems appropriate to assume that the sample from Paraguay has either been sampled from a single species or from several allopatric and replacing ones. The absence of character displacement and the seemingly parallel variation of meristic characters suggest that the samples are conspecific.

THE SITUATION IN BOLIVIA

The sample (= *microcephalum*) from the Bolivian provinces of Santa Cruz de la Sierra and Sara (N=28) represents a single assemblage with low ($R=188-215$, $m=200$) numbers of postpectoral annuli. The head pattern for this group is similar to that of the two variant specimens from Sao Paulo, Brazil, except that the shield-shaped azygous is small and posteriorly restricted in all specimens (fig. 8). The posterior head segments are often darkly pigmented. The pectoral pattern shows no elongate segments but its segments are enlarged and form rows of anteriorly open chevrons. Members of the assemblage show several rows of segments with dark, central pigmentation below the lateral sulci. Similar "spotted" segments occur on the dorsal surface of the tail.

TABLE 2
ANALYSIS OF SYMPATRIC SAMPLES FROM PARAGUAY

	Group 1	Group 2	Group 3
No. of Specimens	19	6	9
Head Segment Pattern	fig. 6A	fig. 6B	fig. 6C
Nos. of Annuli (Anterior Laterals + Postpectorals)	(10-17) + (200-271) (m=243)	(12-14) + (225-265) (m=240)	(11-15) + (226-255) (m=237)
No. of Body Vertebrae	96-104	92-99	96-99
Snout-Vent Length (in mm.) Minimum-Maximum	(164-361)	(141-310)	(225-397)

Neither the segmentation pattern nor any other character examined shows a multimodal distribution, so that there appears to be only a single species in Bolivia.

THE SITUATION IN ARGENTINA

Only individual specimens (*=microcephalum*) are available from the province of Salta (N=4), Formosa (N=1), Chaco (N=4), Misiones (N=1), Corrientes (N=7), Entre Rios (N=4), and Buenos Aires (N=1). A single specimen, M.G. No. 1010.75 bears the label "Rio Negro de Patagonie." The locality is presumably erroneous, as it extends the range of the genus more than 500 kilometers to the south, and because the specimen exhibits Paraguayan rather than southern Argentinian character states. A second specimen, N.M.W. No. 17, attributed to the mouth of the Rio Negro, Argentina, exhibits character states diagnostic of a distinct group of specimens (*polystegum*) from northeastern Brazil. Hence these specimens were omitted from the analysis. Also omitted were specimens labeled only "Argentina" and one labeled "Uruguay."

All the samples had postpectoral counts that fell between 185 and 227 (m=206). The specimens from Salta showed the head and pectoral pattern variations noted in Bolivia. One specimen from Formosa, adjacent to Paraguay, and another from the central Chaco (fig. 7) have the head and pectoral patterns characteristic of the first Paraguayan group (fig. 6A), whereas their postpectoral counts (215, 225) were relatively high. The remaining 17 specimens, collected near the eastern borders of Argentina, have a cephalic pattern characterized by a more or less shield-shaped azygous whose anterior tip is in or near contact with the rostronasal, and by very

wide supraocular segments. The pattern thus reminds one of that noted for the specimen from Fazenda Ipanema, Sao Paulo (fig. 5). The postpectoral counts and other meristic data of this assemblage suggest a unimodal distribution.

Nothing in the above pattern suggests that there is more than a single species in Argentina.

THE SITUATION IN MATO GROSSO AND GOIÁS

The seven specimens from west-central Brazil fall into three groups. Three individuals from the border of Bolivia resemble the Bolivian specimens (*=microcephalum*) in head pattern, low postpectoral (R=177-185, m=180.7) counts, and pectoral pattern. The remaining four specimens come from localities either 500 kilometers northeast or southeast of those from western Mato Grosso. They differ markedly from the western samples. The two individuals from the Barra do Tapirape (*=infraorbitale?*) and one from Chapada in central Mato Grosso have significantly larger postpectoral counts (238, 248, 251) than the former, as well as a distinct head pattern that includes very small first supralabials and an azygous that is wider than long. The single specimen (*=L. species*) from Aragarças, Goiás (M.P.E.G. No. 1185) also has a small first supralabial, but differs in a number of other details of head segmentation. Its number of postpectoral annuli (314) is significantly higher than that of any of the other specimens (further discussion under *L. infraorbitale*).

Although the several samples are hardly sympatric, the differences between them are still sufficient to suggest that they represent separate species. Decision on this point is delayed to the section on the "Recognition of species in space."

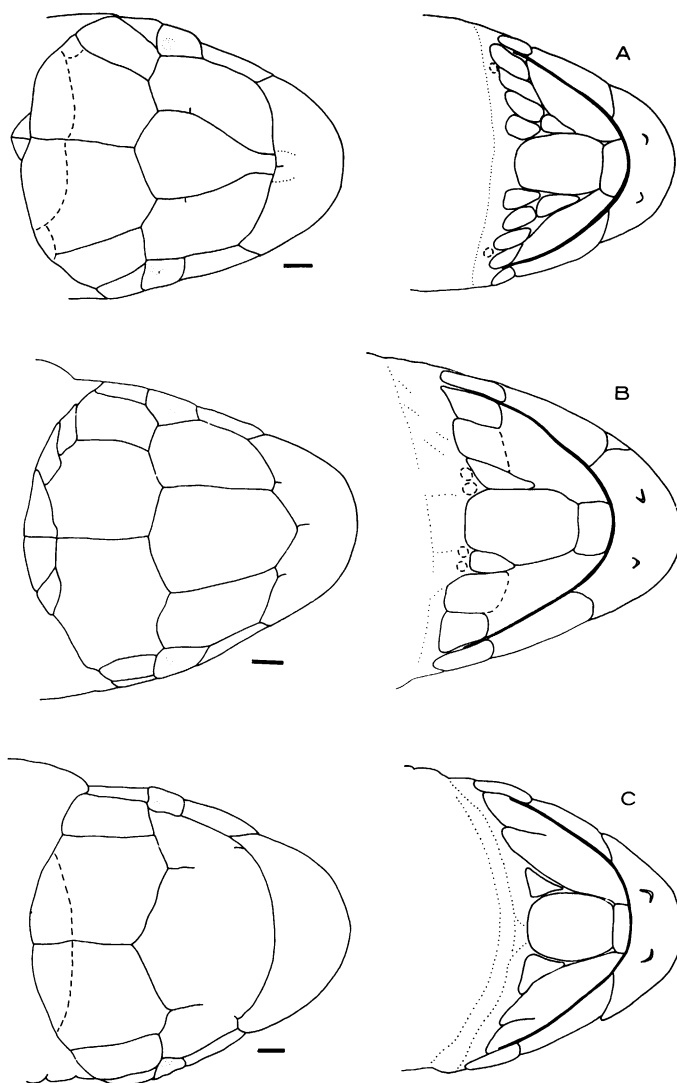


FIG. 6. *Leposternon microcephalum*. Three patterns of head scalation in specimens from Paraguay. A. Group 1, dorsal and ventral views. B. Group 2, dorsal and ventral views. C. Group 3, dorsal and ventral views. Dotted lines indicate areas of folding. Lines equal 1 mm. to scale.

THE SITUATION IN MINAS GERAIS AND ESPIRITO SANTO

Some 14 specimens are available from the southeastern portion of Minas Gerais and the state of Espirito Santo. These specimens (table 3) clearly fall into four groupings, which parallel quite closely those considered to represent good species in the analysis of the sample from Rio de Janeiro. The main difference is in the relative

frequency in which the forms occur in the sample, thus the ratio (of *microcephalum* to *scutigerum* to *infraorbitale* to *wuchereri*) is 95/7/1/1 in Rio de Janeiro and 9/1/4/1 in the present sample. The change is sufficiently drastic to indicate that the forms probably occupy distinct ecological, and probably microgeographical, areas which were presumably sampled unevenly.

The records confirm that the four groups noted in Rio de Janeiro represent distinct species.

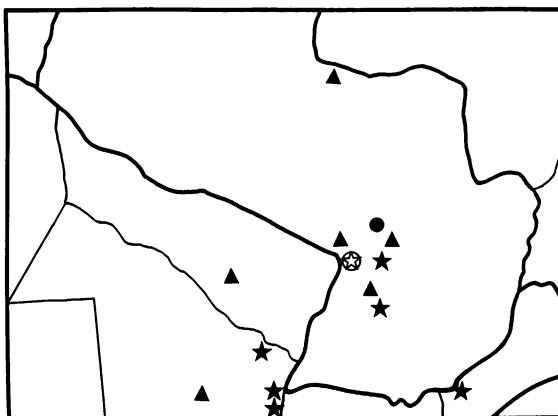


FIG. 7. *Leposternon microcephalum*. Distribution of head-pattern variants in Paraguay and vicinity. Stars refer to those represented by figure 6A, triangles to those of figure 6B, and circles to those of figure 6C.

THE SITUATION IN BAHIA

Of the 15 specimens from Bahia only four bear exact localities. Four groups may be recognized from the composite assemblage by comparison of postpectoral counts and the arrangements of head and pectoral shields; three of these show non-overlap in vertebral numbers (table 4).

The first group (*=microcephalum*) has low postpectoral counts and is otherwise similar to the Rio-low group. Next are four specimens (*=infra-orbitale*) differing from group one in head pattern

(type C of fig. 3, rather than type A), in the presence of a small first supralabial, in the number of anterior laterals and postpectorals, and apparently in larger body size. The third group consists of a single specimen (*=wuchereri*) with a postpectoral count in the range of those of group two, but differing in having a peculiar pectoral pattern composed of three to four pairs of enlarged and elongate shields, as well as a cephalic pattern distinguished by an azygous shield that touches the rostronasal, and the

TABLE 3
ANALYSIS OF SYMPATRIC SAMPLES FROM MINAS GERAIS AND ESPIRITO SANTO

	Group 1	Group 2	Group 3	Group 4
No. of Specimens	9	1	4	1
Head Segment Pattern	fig. 3A, 4A	fig. 3B, 4B	fig. 3C, 4C	fig. 3D, 4D
Nos. of Annuli (Anterior Laterals+Postpectorals)	(11-15)+(198-226) (m=208)	12+306	(12-19)+(242-255) (m=249)	14+245
No. of Body Vertebrae	97-103	121	96-99	120
Snout-Vent Length (in mm.) Minimum-Maximum	(153-470)	500	(474-635)	314
Pectoral Pattern	Enlarged pair of segments on midline; additional pairs, elongated or enlarged, which slant toward these median segments	3 pairs of greatly enlarged segments; hourglass- shaped pattern	Slightly enlarged segments in rows slanting to indistinct midline	3-4 pairs of elongated segments partially fused with one another

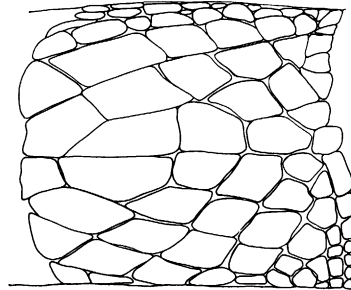
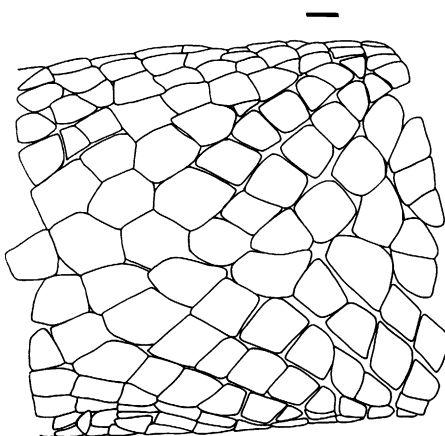
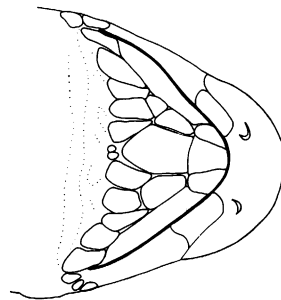
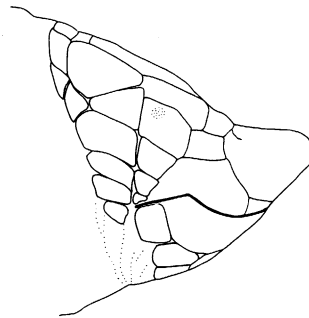
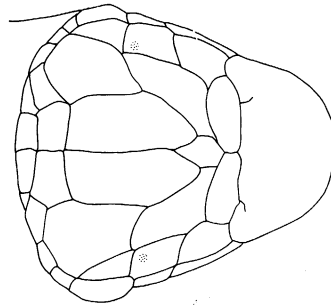
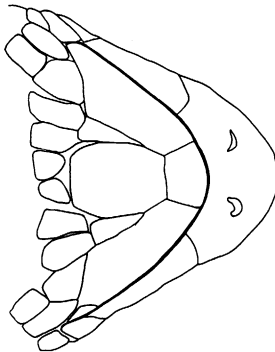
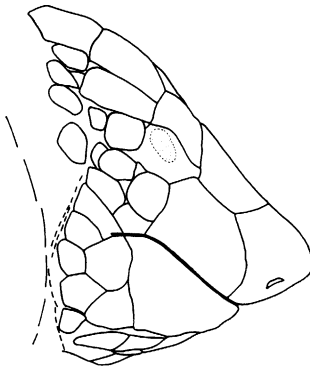
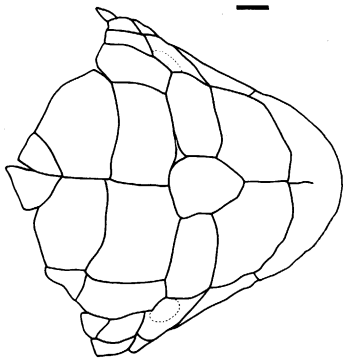


FIG. 8. *Leposternon microcephalum* (left). Pattern of head scalation. Dorsal, lateral, and ventral views, and pectoral scalation of M.A.C.N. No. 3217, from "Bolivia." Dotted lines indicate areas of folding. Line equals 1 mm. to scale.

FIG. 9. *Leposternon polystegum*. Pattern of head scalation. Dorsal, lateral, and ventral views, and pectoral scalation of U.M.M.Z. No. 103078, from Barreiras, Bahia, Brazil, characteristic of Group 4. Dotted lines indicate areas of folding.

absence of a small first supralabial. The last two specimens (*=polystegum*) have significantly higher postpectoral counts than any others from Bahia and differ even more markedly in having a distinct cephalic pattern (fig. 9). The most notable aspects of this are a medium-sized first supralabial followed by a very large second one, a much-enlarged rostronasal followed by much wider than long prefrontals, a tiny azygous, and a pair of narrow and elongate frontals that reach well anterior of the level of the eyes. The pectoral pattern is characterized by a general enlargement, rather than a fusion, of the segments.

Only the first and the third of the four morphologically recognizable groups are recorded from the same locality (Andarai, Bahia). Yet the degree of morphological difference seems to make it certain that the remaining two groupings were also sampled from distinct species. One may then recognize four good species in the state of Bahia.

THE SITUATION IN PERNAMBUCO AND RIO GRANDE DO NORTE

Seven of the 11 specimens from these states lack exact locality data. Three patterns are noted (table 5). The first (*=microcephalum*) found in an individual specimen from Pernambuco is characterized by a low number of postpectorals, a medium number of vertebrae, and the cephalic segmentation pattern of the Rio-low assemblage with which it otherwise agrees. The second

(*=infraorbitale*) is also known from only a single specimen from Pernambuco. It differs in its distinct head segmentation (pattern 3C rather than 3A), small first infralabial, a higher count of postpectorals, and a larger total size, but its vertebral count is not significantly different from that of the first. The remaining nine specimens (*=polystegum*) from Pernambuco and Rio Grande do Norte exhibit a third and distinct cephalic pattern (fig. 9). In addition they exhibit much higher counts of postpectoral annuli and vertebrae.

Consequently there seem to be three distinct species in this region.

THE SITUATION IN PARÁ AND AMAZONAS

There are seven specimens available for comparison from Pará (two of these were not available when this report was being written), but only one of the specimens has locality data. Two groupings may be recognized (table 6). Three specimens from Pará and the one from Amazonas (*=microcephalum*) show low postpectoral counts and the cephalic and pectoral pattern of the Rio-low group. Four specimens (*=polystegum*) have high postpectoral counts, significantly higher numbers of vertebrae, and a distinct cephalic and pectoral pattern (cf. fig. 9).

Consequently there appear to be two good species in this region.

TABLE 4
ANALYSIS OF SYMPATRIC SAMPLES FROM BAHIA

	Group 1	Group 2	Group 3	Group 4
No. of Specimens	8	4	1	2
Head Segment Pattern	fig. 3A, 4A	fig. 3C, 4C	fig. 15	fig. 9
Nos. of Annuli (Anterior Laterals + Postpectorals)	(11-15) + (190-214) (m=205)	(14-18) + (236-275) (m=252)	17 + 265	15 + (306-324) (m=315)
No. of Body Vertebrae	93-102	99	120	138-135
Snout-Vent Length (in mm.)	(285-480)	(334-581)	348	(375-384)
Minimum-Maximum				
Pectoral Pattern	Elongated pair of segments on midline; additional pairs, elongated or enlarged, may slant toward these median segments	3 pairs of greatly enlarged segments; hourglass-shaped pattern	Slightly enlarged segments in rows slanting to indistinct midline	3-4 pairs of elongated segments, partially fused with one another

SUMMARY

The analysis of non-dimensional species suggests that there are at least four distinct species within the genus, as four forms could be recognized in the comparisons for Rio de Janeiro, Minas Gerais, and Espirito Santo, and Bahia. The distribution of cases of sympatry is of

further interest as it suggests sympatry of at least two and usually three or four forms in all localities north of Sao Paulo and east of Goiás. In contrast, there is no case of sympatry south or east of this line, even though the samples from the south are at least as large and generally significantly larger.

TABLE 5
ANALYSIS OF SAMPLES FROM PERNAMBUCO AND RIO GRANDE DO NORTE

	Group 1 (B.M. No. 1903.12.3.8)	Group 2 (M.G. No. 1010.77)	Group 3
No. of Specimens	1	1	9
Head Segment Pattern	fig. 3A, 4A	fig. 3C, 4C	fig. 9
Nos. of Annuli (Anterior Laterals + Postpectorals)	15 + 212	17 + 237	(16-18) + (244-282) (m=266)
No. of Body Vertebrae	100	95	122-135
Snout-Vent Length (in mm.) Minimum-Maximum	324	480	(240-332)
Pectoral Pattern	Elongated pair of segments on midline; additional pairs, elongated or enlarged, may slant toward these median segments	3 pairs of greatly enlarged segments; hourglass-shaped pattern	Slightly enlarged segments in rows slanting to indistinct midline

TABLE 6
ANALYSIS OF SPECIMENS FROM PARÁ AND AMAZONAS

	Group 1	Group 2
No. of Specimens	4	4
Head Segment Pattern	Fig. 3A, 4A	Fig. 9
Nos. of Annuli (Anterior Laterals + Postpectorals)	13 + (192-211) (m=201)	(14-18) + (335-348) (m=335)
No. of Body Vertebrae	97-105	133
Snout-Vent Length (in mm.) Minimum-Maximum	(166-360)	(205-432)
Pectoral Pattern	Elongated pair of segments on midline; additional pairs, elongated or enlarged, may slant toward these median segments	3 pairs of greatly enlarged segments; hourglass-shaped pattern

RECOGNITION OF SPECIES IN SPACE

METHOD OF APPROACH

IT BECOMES OF INTEREST NOW to ask which of the forms defined as discrete in the various preceding analyses may be conspecific. Such analysis is simple when the species concerned exhibit little geographical variation. In contrast, the difficulty is magnified when the available samples exhibit considerable geographical variation and are furthermore allopatric.

The simplest way of proceeding is to separate out and to consider conspecific those previously characterized groupings that share one or more major and unique character states. These seemingly associated assemblies must next be tested to determine whether the states of the remaining, thus far unutilized, characters confirm the pattern. The proposed comparison would show first whether the samples are truly conspecific, and second would disclose the extent and kind of geographical variation that may be seen in conspecific assemblages. Such analysis sometimes suggests the utility of naming infraspecific categories.

The number of specimens available for this analysis is obviously greater than that used for review of non-dimensional species, as there are 150 specimens lacking locality or assigned only to "Brazil." Such specimens cannot provide evidence about geographical variation, but may offer information about the total range of variation of each group. They were therefore included whenever a species had been characterized by the non-dimensional and species in space approach. The composite group may then be large enough to permit utilization of characters whose internal variation was too great to allow their use to discriminate between samples of very small size. The utility of this procedure is indicated by the confirmation of another species on the basis of the "no-data" collection; it is obvious, however, that it would have less merit in a group whose range and variability were better documented by specimens with adequate geographical data.

This section will serve as the basis on which the conclusions presented herein may be tested when additional specimens come to hand. The section is hence organized under the names ulti-

mately assigned to the populations, and the data are presented in a standard descriptive scheme (Gans, 1966). The presentation is designed to permit the rapid test of the concordance of new specimens with the views expressed.

Leposternon scutigerum

SELECTION AND SOURCE

The specimens initially classified as Rio-high show the most strikingly distinct head and pectoral pattern, are easiest to recognize, and consequently are discussed first. Their head segmentation (figs. 3B, 9) is unique in having the cephalic area covered with only two very much enlarged and almost always keratinized shields. (A single row of much smaller and non-keratinized segments fringes the occipital region).

Besides three localities relatively close to the city of Rio de Janeiro and included in Rio-high, the Minas Gerais and Espirito Santo sample included one specimen with this pattern from southern Minas Gerais, a locality generally northwest from the coastal records. Twenty-nine other specimens lack locality data.¹

VARIATION

The composite sample agrees in having at least four pairs of enlarged pectoral segments, the two medial pairs presenting a characteristic hourglass shape (fig. 10). Even more diagnostic than the enlargement of the pectoral segments is their irregularity. None of them is either trapezoidal or parallelogrammic in shape. The species has a characteristically high number ($R = 117-129$) of body vertebrae.

The assemblage is too small to permit discussion of geographical variation, except to note that the single specimen from Minas Gerais has uniquely high numbers of postpectoral annuli with the distinction more readily apparent for dorsal than for ventral counts (fig. 11). The

¹Guichenot (1855) noted a specimen of this form collected by de Castelnau "sur les bords de l'Araguay, province de Goyaz." The only pertinent specimen appears to be M.H.N.P. No. 3126 listed as "Castelnau-Deville, Brasil, No data." Its characteristics are in good agreement with those of specimens from the vicinity of Rio de Janeiro.

specimen from Minas Gerais also represents the extreme portion of the range of character states for counts of anterior laterals and posterior laterals, but its number of body vertebrae lies

almost on the species mean. All specimens had a greater number of ventral than of dorsal segments per annulus. In several of these characters the aggregate range for specimens with locality

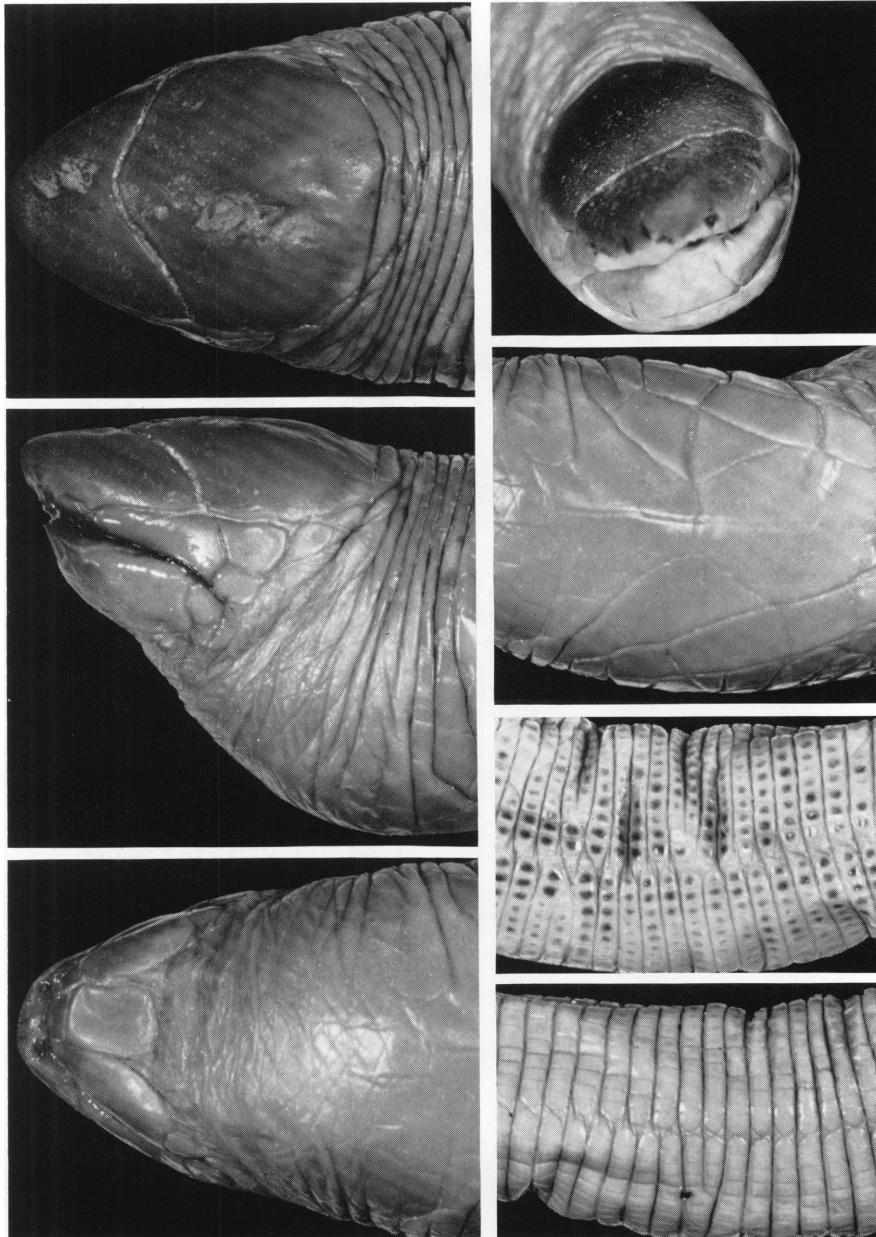


FIG. 10. *Leposternon scutigerum*. Left column: Dorsal, lateral, and ventral views of head of I.M.Z.U.T. No. 326, from Brazil, no locality. Right column: Top, anterior view of head of N.M.B. No. 3817, no locality. Second from top, pectoral region, I.M.Z.U.T. No. 326 from Brazil. Bottom two, segmentation of dorsal and ventral surface at midbody of Z.M.U. No. 1399, from Brazil, no locality.

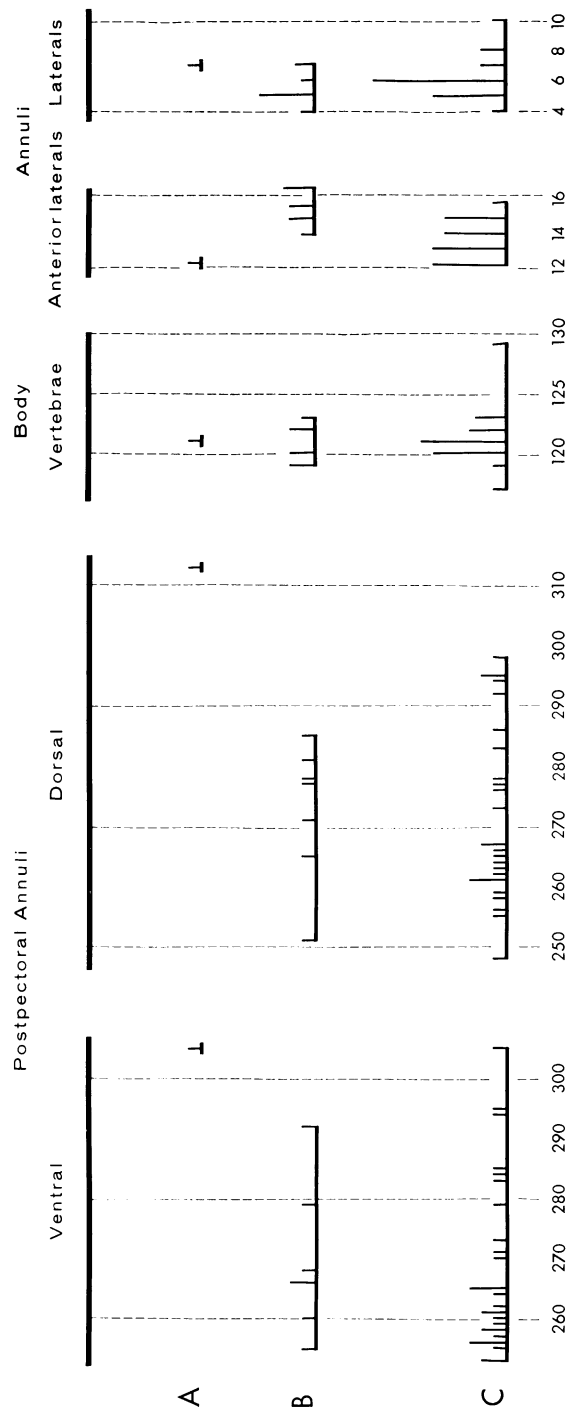


FIG. 11. *Leposternon scutigerum*. Bar diagram comparing samples from (A) Minas Gerais, (B) Rio de Janeiro, and (C) "No Locality," for numbers of ventral and dorsal postpectoral annuli, body vertebrae, anterior lateral annuli, and lateral annuli.

is exceeded by that for specimens lacking locality.

Although the range of variation for post-pectoral annuli observed within the composite sample is considerably higher than that previously observed in *Amphisbaena*, the comparison of such large and obviously conspecific samples as those from Santa Catarina suggests that this

may not be unusual in *Leposternon*. Certainly the variation in number of body vertebrae is comparable with the range observed in *Amphisbaena*. Hence there is little doubt that we are dealing with a single species and that this presumably shows considerable geographical variation, the presence of which can be noted but which cannot now be characterized.

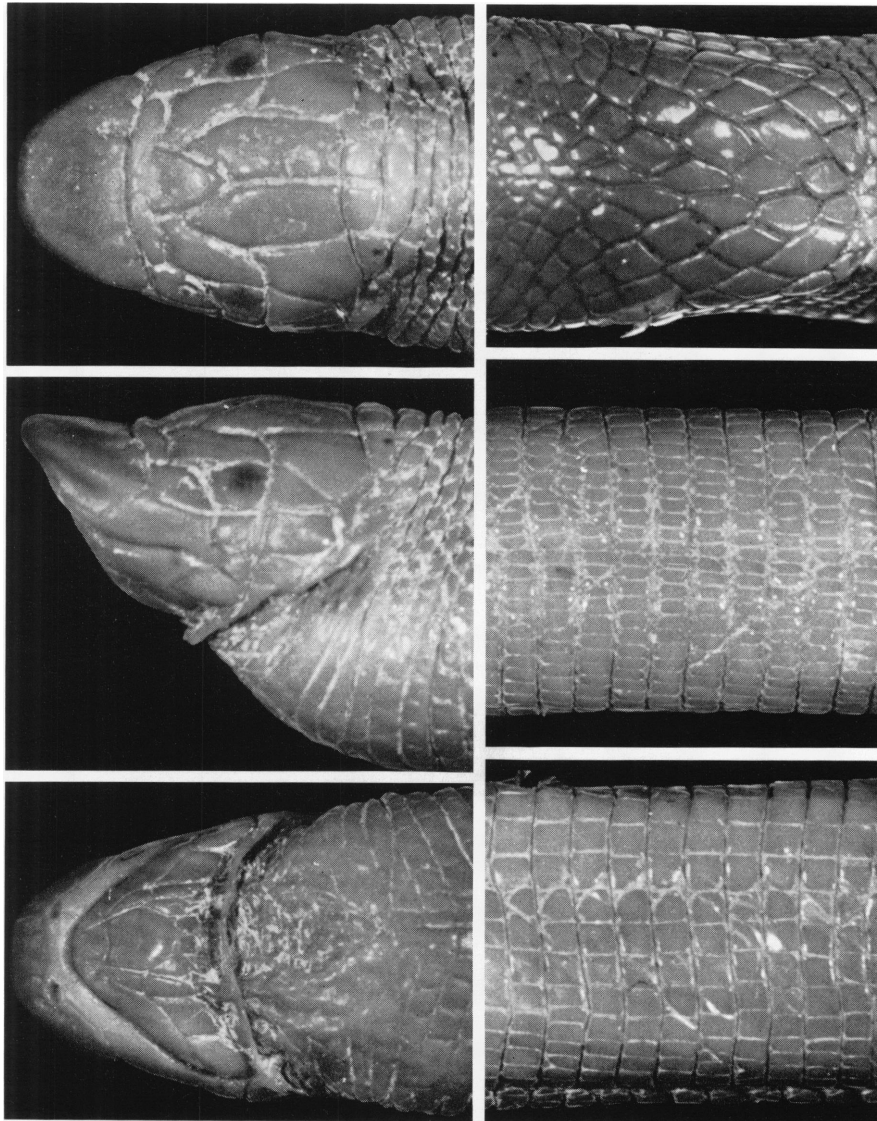


FIG. 12. *Leposternon polystegum*. Left column: Dorsal, lateral, and ventral views of head of M.G. No. 1010.79, from Brazil, no locality. Right column: Top, pectoral region of Z.M.U. No. 1397B, from Brazil, no locality. Middle and bottom, segmentation of dorsal and ventral surfaces at midbody of M.G. No. 1010.79, from Brazil, no locality.

Leposternon polystegum

SELECTION AND SOURCE

The two specimens of group four from Bahia are separated out by their very high postpectoral counts and distinct head pattern. Their head segmentation (figs. 9, 12) is characterized by a narrowing and elongation of the frontals, which anteriorly enclose a very small azygous, and reduction in size of the prefrontals, as well as the occurrence of a small pair of first supralabials and of a pair of small first infralabials. There is a sharp groove or bend at the junction of the rostronasal with the more posterior head shields. The rostronasal, but not the more posterior head shields, is almost always keratinized.

Equivalent head patterns are also shown by group three from Pernambuco and Rio Grande do Norte, by group two from Pará (fig. 13), and by eight specimens lacking any locality data (including one specimen attributed to the mouth of the Rio Negro, Argentina). These specimens also show high postpectoral counts, although the counts have an extensive range ($R=80$). The relatively high (122–141) counts of body vertebrae have a significantly lower range ($R=19$).

All specimens of this sample have the pectoral region filled with enlarged segments (of reduced number) that are never elongate and are arranged in rows of anteriorly open chevrons (fig. 9). All specimens, furthermore, have from zero to eight more dorsal than ventral segments per annulus, and show a faint but definite precloacal pore on each side of the precloacal shield.

VARIATION

There is considerable variability in the shape and arrangement of the segments along the posterior junction of the rostronasal. The two prefrontals may fuse completely or in part with the azygous or alternately with the pair of segments immediately posterior to them. The azygous may contact the rostronasal and its size varies by a factor of four. All but one of the specimens from Rio Grande do Norte and Pernambuco have the azygous in broad contact with the rostronasal; in specimens from Pará and Bahia there may be point contact but the rostronasal is more commonly excluded by contact between the prefrontals.

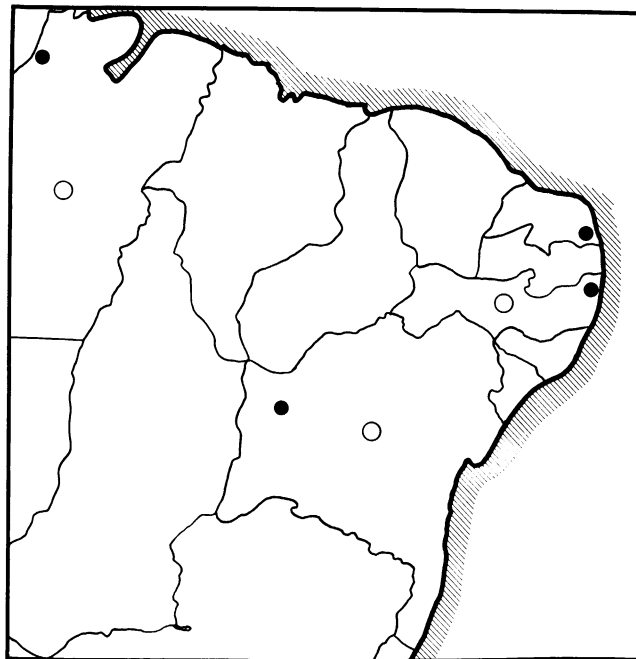


FIG. 13. *Leposternon polystegum*. Distribution of species. Solid dots indicate records, open circles refer to states to which specimens have been ascribed. Compare with figure 1.

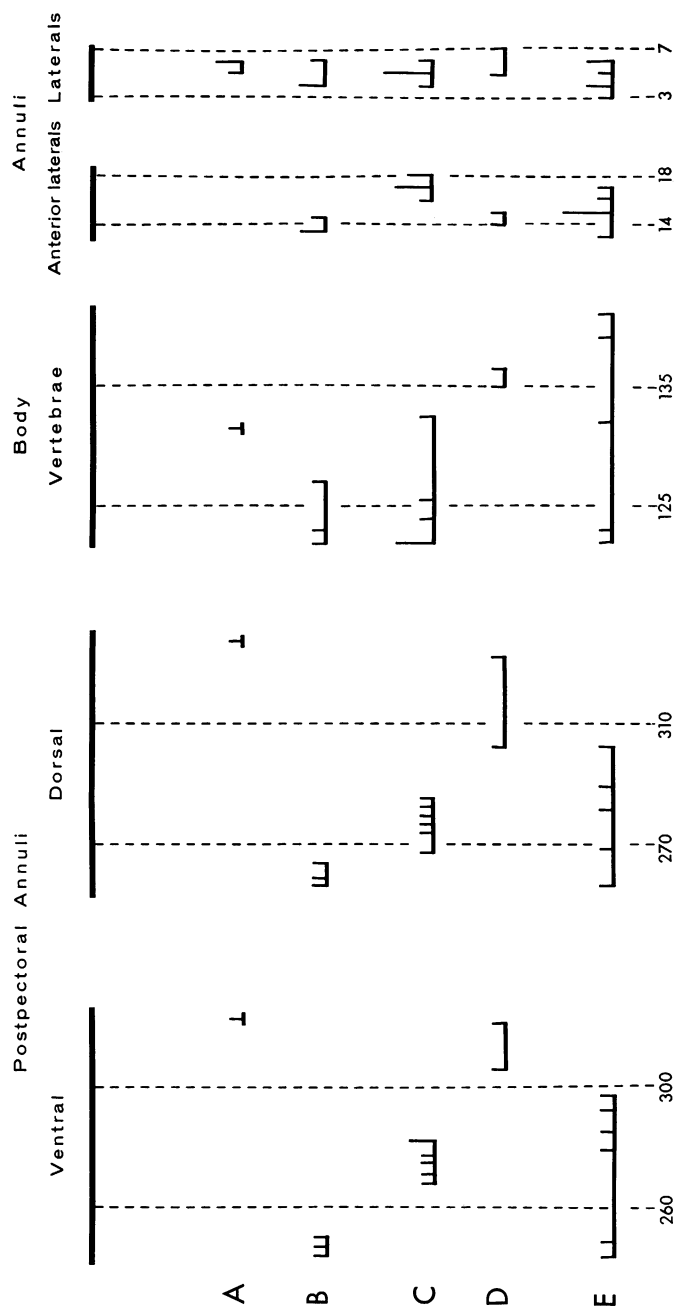


FIG. 14. *Leposternon polystegum*. Bar diagram comparing sample from (A) Pará, (B) Rio Grande do Norte, (C) Pernambuco, (D) Bahia, and (E) "No locality," for numbers of ventral and dorsal postpectoral annuli, body vertebrae, anterior lateral annuli, and lateral annuli.

Although the postpectoral counts of these specimens are always high ($R=244-324$, $m=278$), three seemingly non-overlapping, geographically separated groups are noted (fig. 14). Thus, the Rio Grande do Norte specimens have low ($R=244-250$, $m=247$) counts of postpectoral annuli, those from Pernambuco have intermediate ($R=268-282$, $m=275$) counts, and those from Bahia have high ($R=306-324$, $m=315$) counts. Unfortunately, postpectoral

counts are lacking for the three specimens from Pará; one specimen is damaged and the counts for the other two were recorded together with those of anterior laterals. Yet, it would appear that Pará specimens are in the high range as the available counts are very high. What is interesting is that the numbers of body vertebrae reflect the same pattern much more faintly. The variation is thus in the number of dermal annuli per vertebra, rather than in the vertebral number

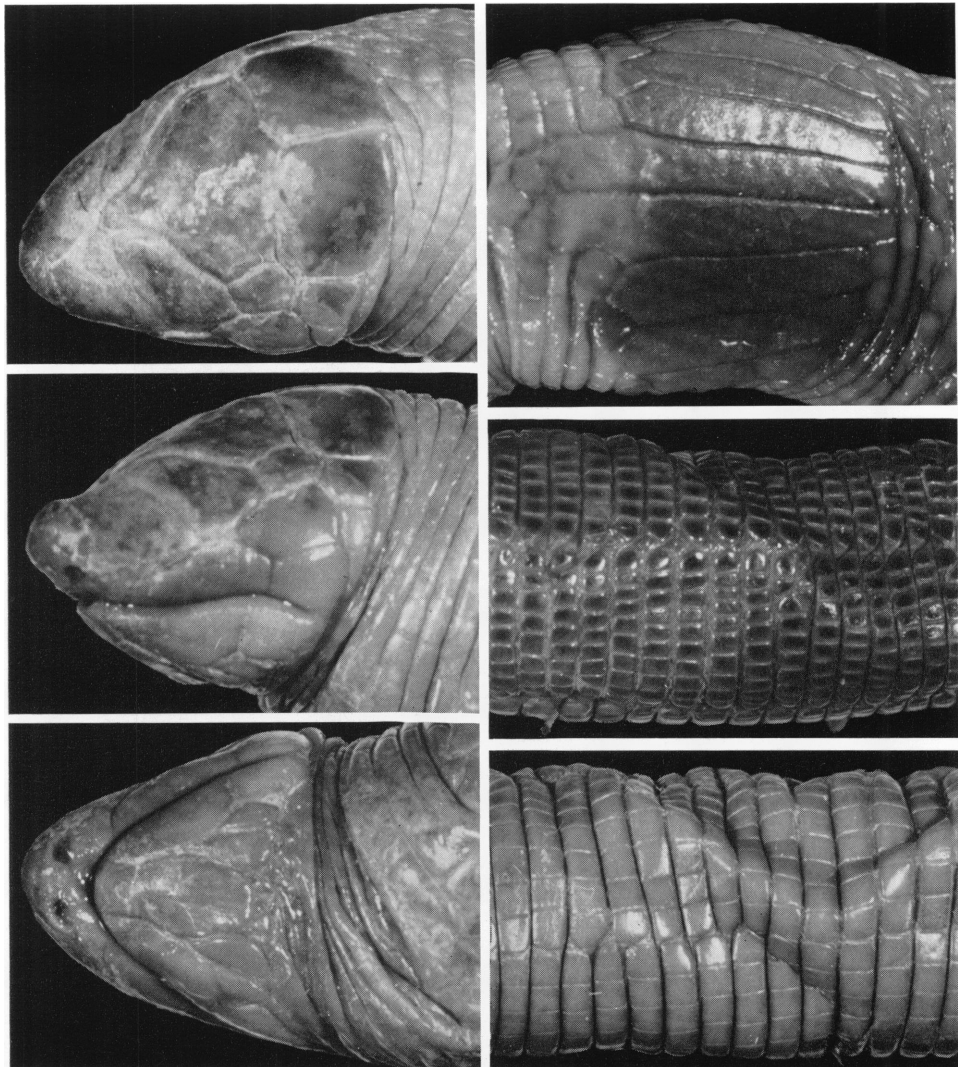


FIG. 15. *Leposternon wuchereri*. Left column: Dorsal, lateral, and ventral views of head of Z.M.U. No. 9389, from Andaraí, Bahia, Brazil. Right column: Pectoral region of N.M.W. No. 12373, from Porto Seguro, Bahia, Brazil, and dorsal and ventral views of midbody of Z.M.U. No. 9389, from Andaraí, Bahia, Brazil.

per se. Specimens with no locality span the composite range of postpectoral annuli ($R=253-297$, $m=277$).

Data for numbers of dorsal postpectorals and, to a lesser extent, of segments per annulus also show geographical variation. Unfaded specimens have the pigment evenly distributed over segments of the dorsal and lateral aspects and pigmentation often extends to the dorsal head segments.

The present samples are apparently drawn from a single species that shows considerable geographic variation in meristic characters. It is also possible that the several areas are each inhabited by closely similar, yet replacing species, but such a hypothesis cannot be tested with the present disjunctly distributed samples.

Leposternon wuchereri

SELECTION AND SOURCE

A single specimen with an "intermediate" number of postpectoral annuli (242) and a unique head pattern consisting of but four rows of cephalic segments (fig. 15) was tentatively considered to belong to a distinct species during analysis of the sample from Rio de Janeiro. The head segmentation of this individual is further characterized by a broad azygous that sends a narrow extension between the prefrontals to contact the rostronasal (fig. 3D).

Five additional specimens show a similar pattern of cephalic segments (figs. 15, 16). Only one of the two separated out in the comparison for Bahia-Espirito Santo has locality data, namely Andaraí, Bahia. Another refers only to Espírito Santo; a third attributed to "Porto Seguro" may be of that city in the state of Bahia. The fourth and fifth¹ lack any locality.

VARIATION

The composite sample agrees in having three to four pairs of elongate pectoral segments that may be fused and often lie parallel to one another.

This small sample of five specimens is remarkably consistent in its meristic characters. The numbers of postpectoral annuli ($R=242-265$) show little dispersion from the mean (252) number. The number of body vertebrae ($R=$

¹An unnumbered G.U.M. specimen was discovered after the present paper was completed but was not used in the analysis.

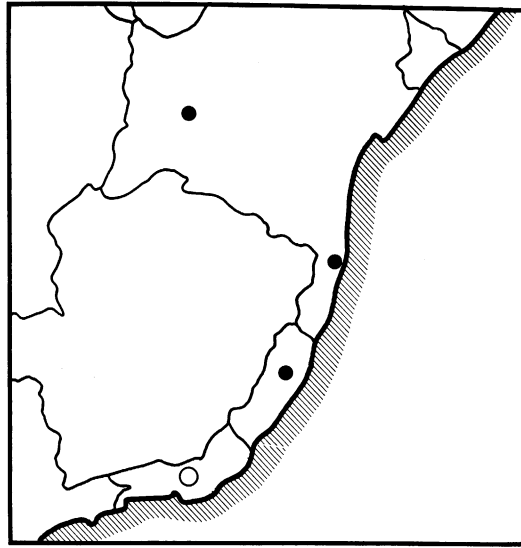


FIG. 16. *Leposternon wuchereri*. Distribution of species. Solid dots indicate records; open circles refer to states to which specimens have been ascribed. Compare with figure 1.

118-122) is remarkably constant. The low numbers of dorsal segments per annulus are very close to, or one to two less than, the ventrals. Both tend to be near 20. The counts of anterior laterals, posterior laterals and cloacals are similarly uniform (fig. 17). Pigmentation is noted on the center of dorsal and lateral segments.

These five specimens seem to represent a single species that exhibits little geographical variation.

Leposternon infraorbitale

SELECTION AND SOURCE

The unique specimen from Rio de Janeiro with 236 postpectoral annuli has a small first supralabial as well as an infraocular. The dorsal cephalic segments are arranged in five simple rows with the large azygous situated centrally and not in contact with the rostronasal (figs. 3C, 18).

Thirteen other specimens with a small first supralabial and a similar arrangement of the head pattern were found during the comparisons in Minas Gerais and Espírito Santo (group 3), Bahia (group 2), Pernambuco (group 2) and Mato Grosso and Goiás (groups 2 and 3, fig. 19); two more lack any locality. Presumably exact localities are Santa Teresa and Vitória on

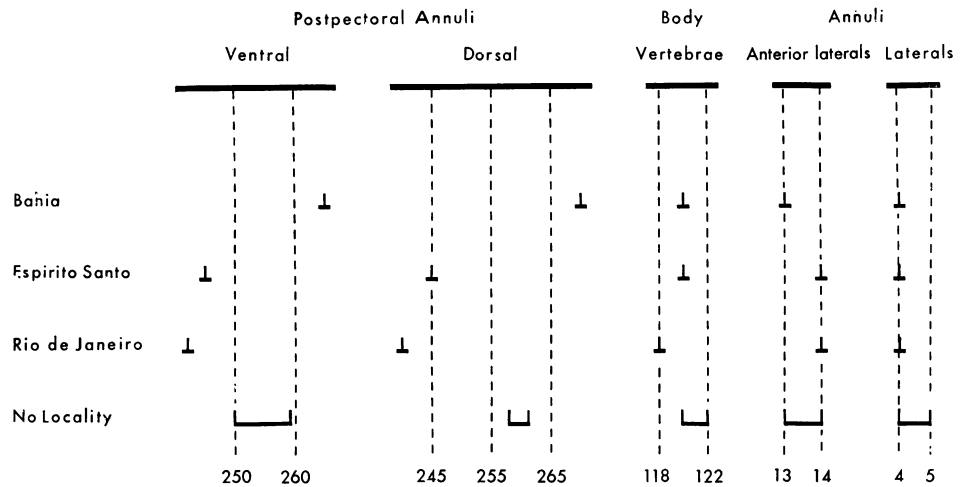


FIG. 17. *Leposternon wuchereri*. Bar diagram comparing samples from Bahia, Espirito Santo, Rio de Janeiro, and "No Locality," for numbers of ventral and dorsal postpectoral annuli, body vertebrae, anterior lateral annuli, and lateral annuli.

Paraizo do Sul, Espirito Santo; Fazenda Paropeba, Minas Gerais; Chapada and Barra do Tapirape, Mato Grosso; and Aragarças, Goiás.

VARIATION

Besides having fairly high counts of postpectoral and low counts of caudal annuli, the composite sample agrees only in the presence of a small supralabial and in the general arrangement of head shields. Three groupings readily become obvious.

All specimens from the eastern portion of this range are notably of large size (snout-vent length, $R=334-635$ mm., $m=581$ mm.) have numbers of postpectoral annuli between 235 and 275 ($m=248$), and numbers of body vertebrae between 95 and 99. These specimens have head patterns similar to specimens from Rio de Janeiro, although the infraocular is absent in two specimens (S.M.F. No. 11847, no locality, and Z.S.M. No. 457, Vitoria, on Paraizo do Sul, Espirito Santo). The pectoral region of the eastern group has scales that are somewhat enlarged, but never elongate or fused (fig. 20). These scales are arranged in anteriorly open chevrons whose apices meet at an indistinct midline. The dorsal scales of a few specimens are faintly and centrally pigmented. Meristic characters do not vary geographically for the eastern group and there are one to six fewer

dorsal than ventral segments per annulus (fig. 21).

The two specimens (A.M.N.H. Nos. 93447 and 93448) from Barra do Tapirape, and one (A.N.S.P. No. 13004) from Chapada, Mato Grosso agree with the eastern specimens in numbers of postpectoral annuli (238, 248, 251) and body vertebrae (95, 99, 100). They are, however, smaller (two have a snout-vent length of 285 mm., one of 190 mm.), exhibit a less angular azygous, and lack infraocular scales. The specimens from Barra do Tapirape have a pectoral pattern with an enlarged pair of median segments (figs. 20, 22). These recently collected specimens are darkly pigmented both dorsally and laterally.

The one specimen (M.P.E.G. No. 1185) from Aragarças, Goiás has a much higher count of postpectoral annuli both dorsally (314) and ventrally (361) than that of any other specimen in the assemblage (fig. 21). Similarly, the higher number of body vertebrae (109), higher number of segments per annulus, higher number of caudal annuli, and head pattern (fig. 23) suggest that it is distinct from the *infraorbitale* sample.

The large-sized individuals of the eastern assemblage of specimens seem to represent a single species. The Mato Grosso specimens have some distinct characters, particularly in their pectoral pattern, and may represent juveniles or

a geographically variant population. The specimen from Goiás is even more distinct and presumably represents a distinct species. As I dislike erecting a new taxon on a unique specimen, it is here retained *incertae sedis*. Additional specimens from inland areas would certainly be desirable.

SEPARATION FROM *Leposternon microcephalum*

This assemblage poses another interesting

problem. This is the status of the entire assemblage versus the species *L. microcephalum* (discussed in the following section). *Leposternon infraorbitale* and *L. microcephalum* are either sympatric or occupy an overlapping range over much of the east central coast of Brazil, from Pernambuco to Espírito Santo to Rio de Janeiro and inland to Minas Gerais. In this zone (for which we have absolute sympatry demonstrated only for Santa Teresa in Espírito Santo) specimens of the two

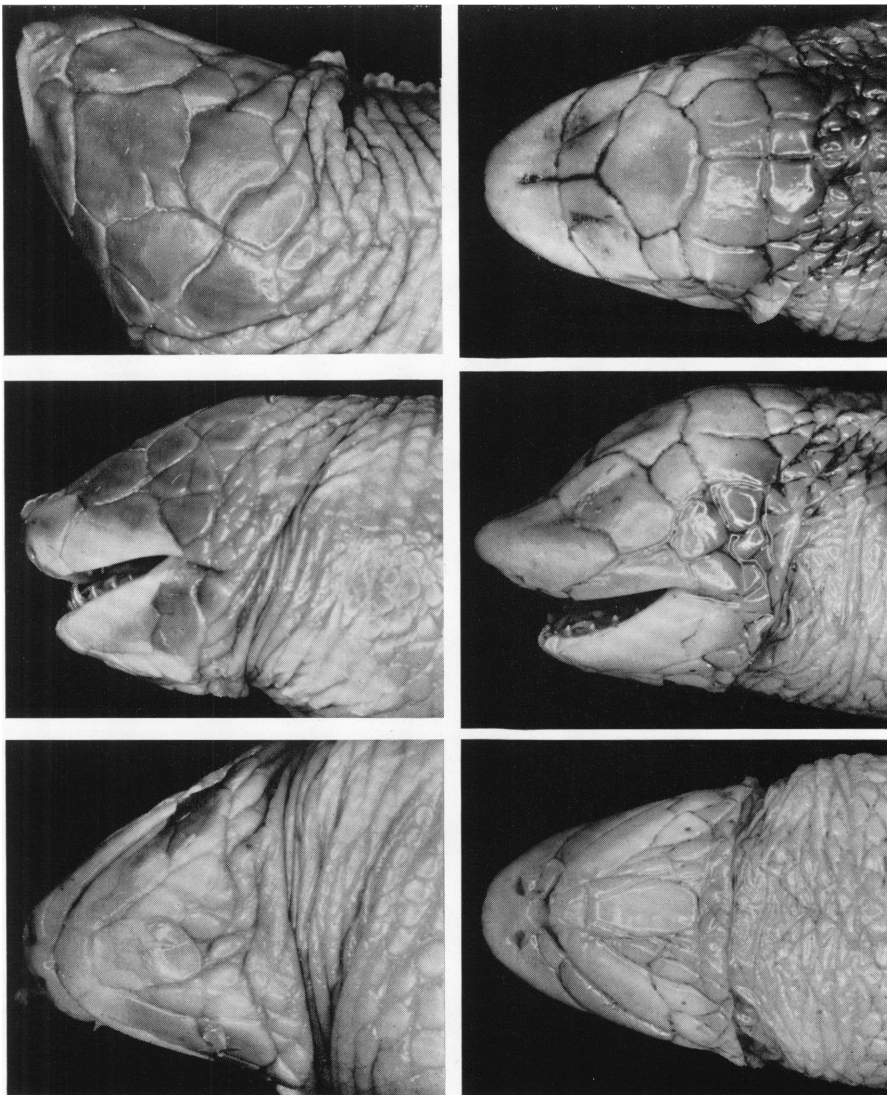


FIG. 18. *Leposternon infraorbitale*. Dorsal, lateral, and ventral views of head. Left column: G.U.M. (unnumbered), from Bahia, Brazil. Right column: A.M.N.H. No. 93447, from Barra do Tapirape, Mato Grosso, Brazil.

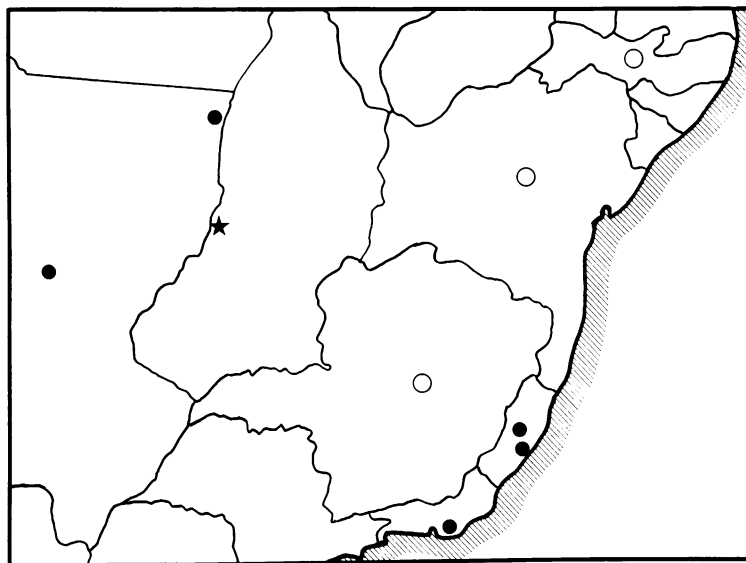


FIG. 19. *Leposternon infraorbitale*. Distribution of species. Solid dots indicate records; open circles refer to states to which specimens have been ascribed. Star refers to Aragarças, site from which a presumably distinct species is reported. Compare with figure 1.

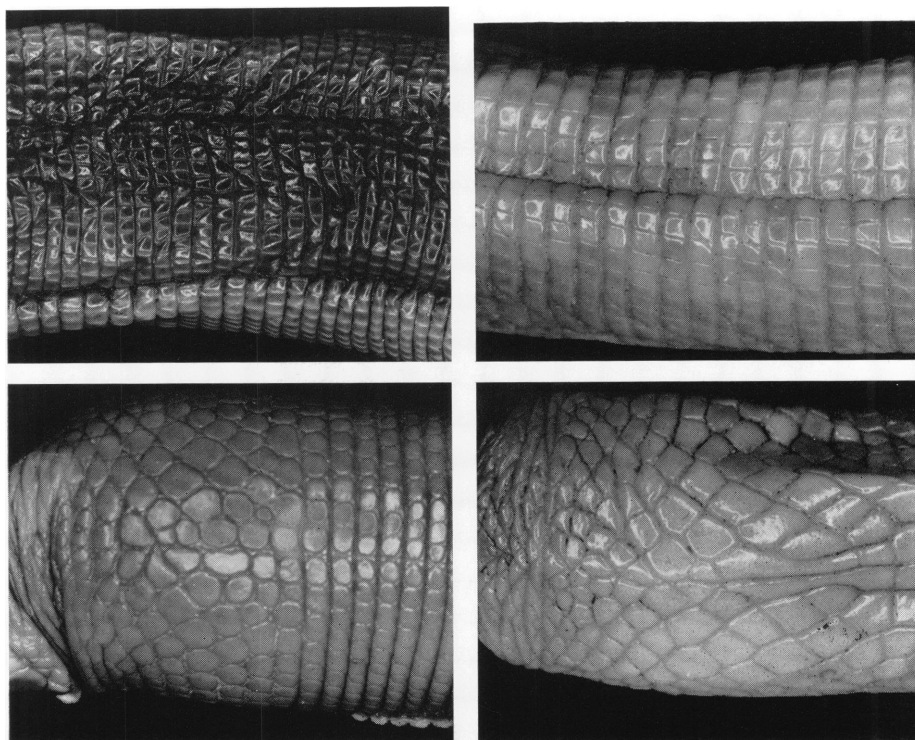


FIG. 20. *Leposternon infraorbitale*. Top row: Dorsal (left) and ventral views of midbody of A.M.N.H. No. 93477, from Barra do Tapirape, Mato Grosso, Brazil. Bottom row: Left, pectoral pattern of G.U.M. (unnumbered), from Bahia, Brazil. Right, pectoral pattern of A.M.N.H. No. 93447, from Barra do Tapirape, Mato Grosso, Brazil.

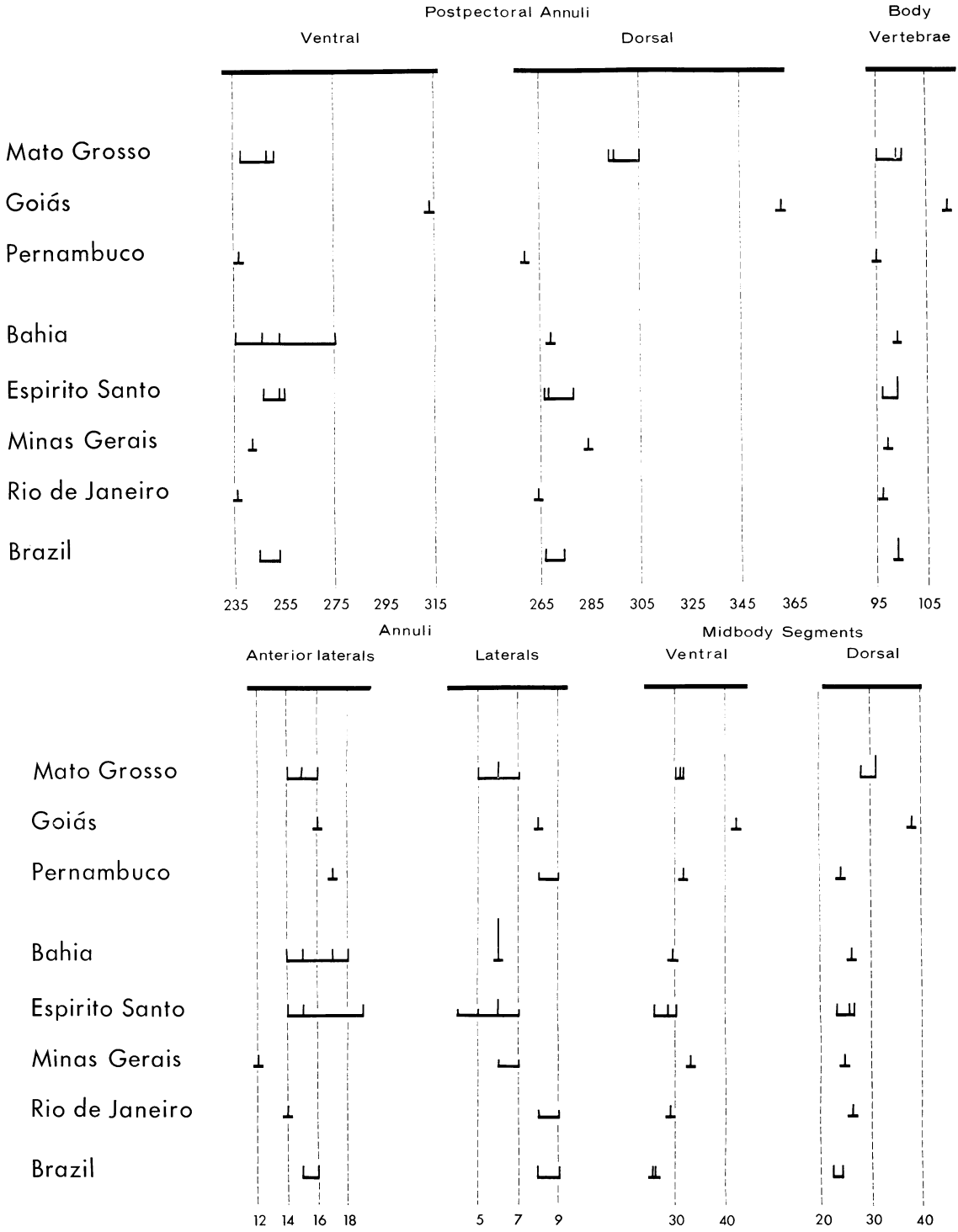


FIG. 21. *Leposternon infraorbitale*. Bar diagrams comparing samples from various localities (top) for numbers of ventral and dorsal postpectoral annuli and body vertebrae; and (bottom) for numbers of anterior lateral annuli, lateral annuli, and mean numbers of dorsal and ventral segments to a midbody annulus. Asymmetrical counts for lateral annuli are indicated by bars one-half the usual height.

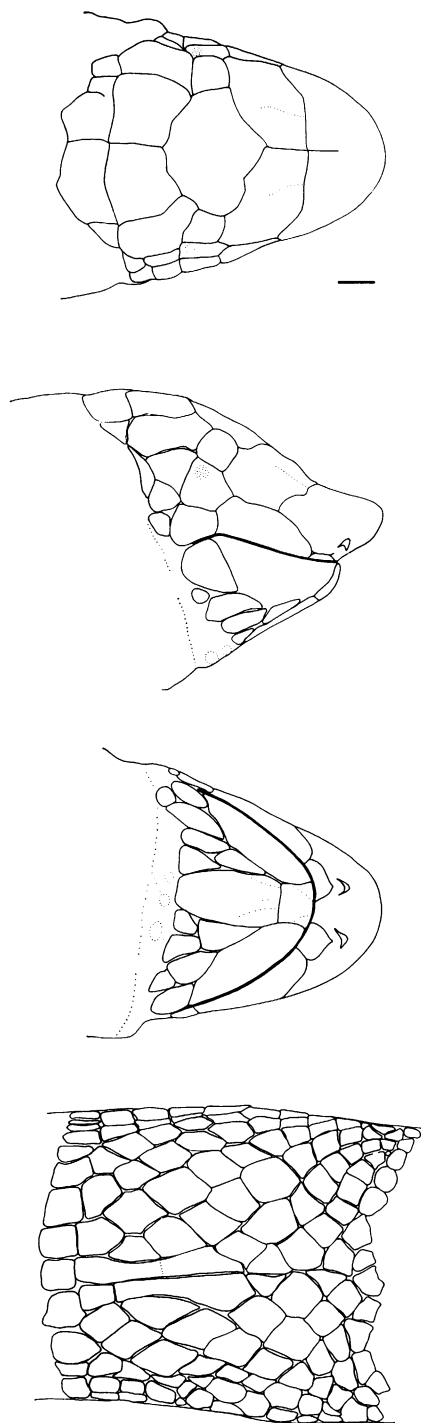


FIG. 22. *Leposternon infraorbitale*. Pattern of head scalation. Dorsal, lateral, and ventral views, and pectoral scalation of A.M.N.H. No. 93447, from Barra do Tapirape, Mato Grosso, Brazil. Dotted lines indicate areas of folding. Line equals 1 mm. to scale.

forms may be differentiated by the consistently higher number of dermal annuli in *L. infraorbitale* and by the occurrence of an infraorbital, of a small first supralabial, of a much more complexly divided preloacal cap, and of a relatively stouter trunk and longer tail in the latter species. At the same time, it seems significant that all specimens of this form are much larger than the mean of *L. microcephalum*; some of them represent the largest amphisbaenians available for this study. On the other hand, no small specimens showing this character pattern have been taken in the zone of presumptive sympatry. Based on this evidence alone, there is little difficulty in recognizing *L. infraorbitale* as a species distinct from *L. microcephalum* even though the two species do not differ significantly in number of body vertebrae.

Two specimens of *L. infraorbitale* from the Barra do Tapirape show a lessening of the differences versus the eastern specimens of *L. microcephalum* (which seems to be absent from Goiás) in their smaller size, more regularly divided preloacal shield, and lack of infraoculars. This leaves only the first small supralabials and counts of postpectoral annuli as indicators of difference.

The distinction between *L. infraorbitale* and *L. microcephalum* will be seen to break down further when comparison is made with the allopatric populations of *L. microcephalum* from Paraguay, which will be shown to have high numbers of postpectoral annuli. Figure 24 shows that the ranges of characteristics for these two species overlap, even though they are almost completely separated in the zone of possible sympatry.

Under the circumstances, it seems most appropriate to consider the pattern as one produced by character displacement in these two forms, which are here considered to represent good species. It seems that differentiation within the jointly occupied area would occur by *L. infraorbitale* occupying a niche for a larger species, with *L. microcephalum* occupying a niche for a smaller species. The possible reduction in size of the Mato Grosso population of *L. infraorbitale*, the larger size of the specimens of *L. infraorbitale* from the remainder of the range, and the larger size of specimens of *L. microcephalum* in southern areas not shared with *L. infraorbitale* reflect responses to the absence or presence of the second species.

Quite apart from the possibility of character displacement is the superficial similarity of these

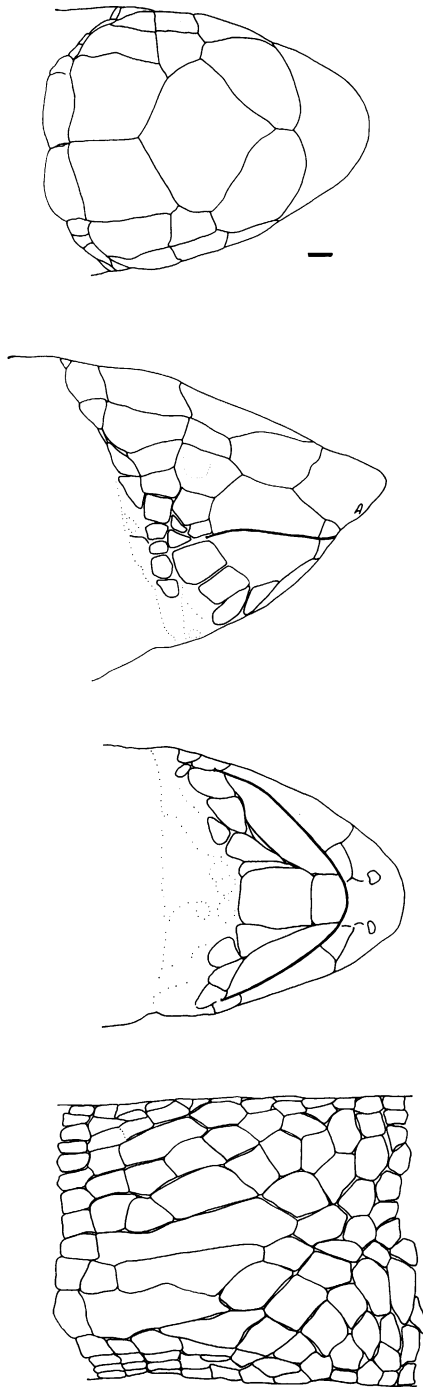


FIG. 23. *Leposternon* species. Pattern of head scalation. Dorsal, lateral, and ventral views, and pectoral scalation of M.P.E.G. No. 1185, from Aragarças, Goiás. Dotted lines indicate areas of folding. Line equals 1 mm. to scale.

two forms, which differ primarily in absolute size. Analysis of their chromosome pattern and of their ecological interactions may well provide interesting results.

Leposternon microcephalum

SELECTION AND SOURCE

It is impossible to separate out any additional groupings from the assemblage remaining after the preceding four categories have been defined. The specimens from Paraguay and from adjacent Argentina (Formosa and Chaco) have generally higher numbers of body annuli and different head patterns. Yet these differences refer to populations that are clearly allopatric to the remaining material, and the comparison of character states may hence proceed for the entire, possibly composite, sample.

Specimens of this assemblage are available from the Brazilian states of Amazonas, Pará, Pernambuco, Bahia, Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, possibly Rio Grande do Sul, and Mato Grosso. Other specimens come from eastern Bolivia, Paraguay, and the northern states of Argentina. Yet a look at the actual records will show that the range is adequately documented for only its east-central portion. Most records from the northern, southern, and western aspects of the range are assignable to states only.

There are also about 110 specimens without locality included in the analysis, although only a limited number of characters were noted for these. In view of the near adequacy of samples from the central area occupied by this assemblage about a hundred or more additional specimens clearly pertaining to this assemblage but also without locality were only checked for general character concordance, but their data were not used for purposes of this study.

VARIATION

HEAD PATTERN—DORSAL: The dorsal cephalic shields of *L. microcephalum* lie in five rows, except for those of specimens from Paraguay (use figs. 25–28 as a guide to the following discussion). Variation in the head pattern is noted primarily in the configuration of the azygous scale and the segments adjacent to it.

The most common pattern (configuration A, fig. 26) is found from Amazonas eastward to

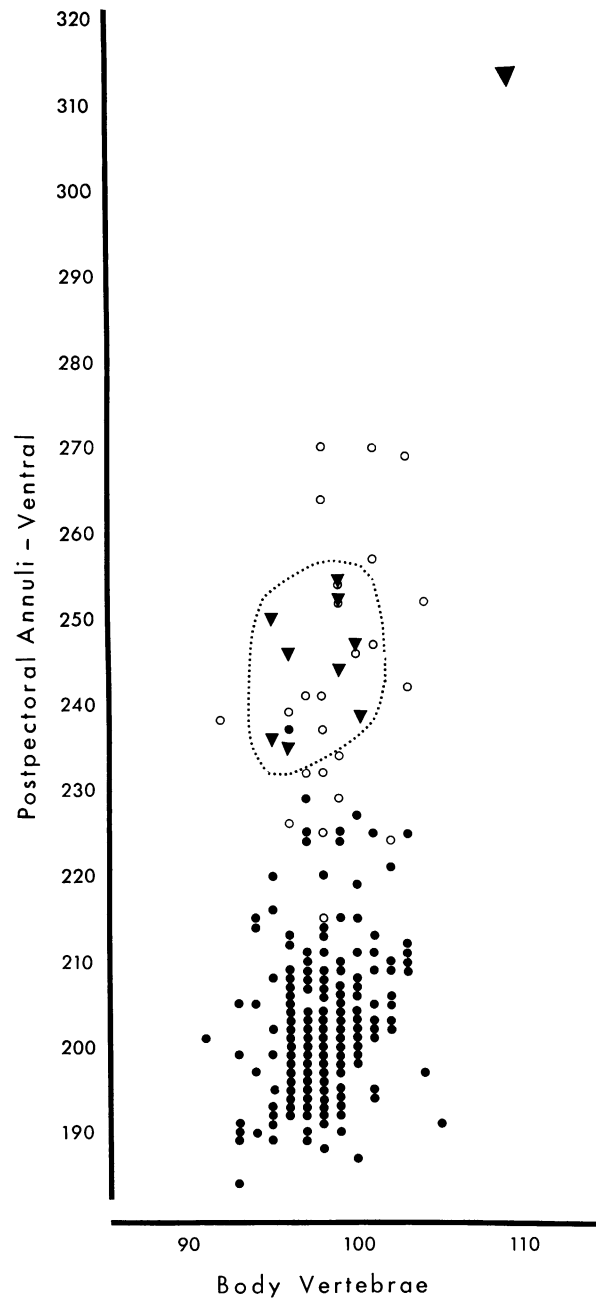


FIG. 24. Scatter diagram comparing number of body vertebrae with number of ventral postpectoral annuli for *L. infraorbitale* (inverted triangles), as well as sympatric (solid circles), and Paraguayan (open circles) samples of *L. microcephalum*. Specimen from Aragarças is shown as a large triangle.

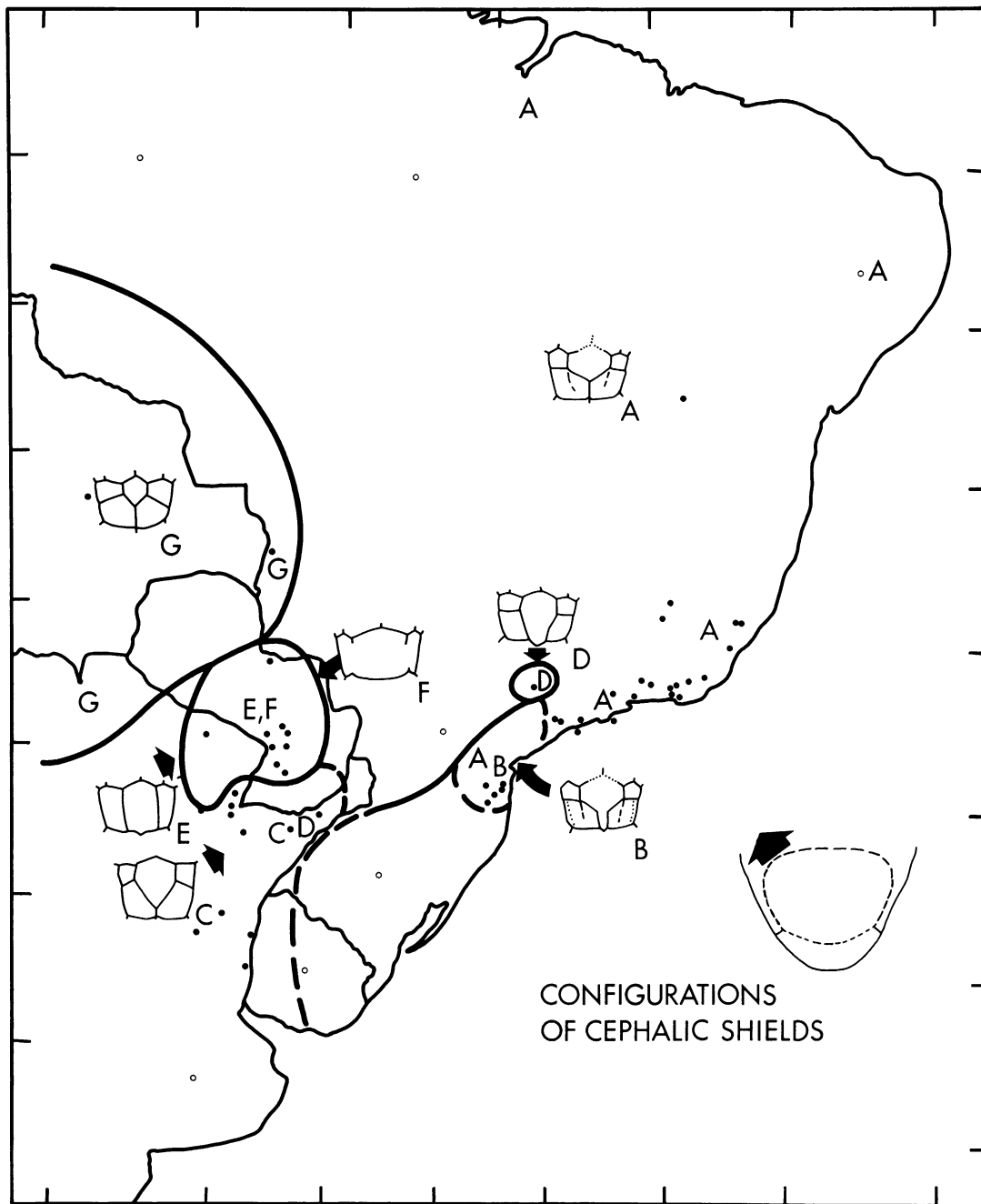


FIG. 25. *Leposternon microcephalum*. Map of range of species showing variance of raphe arrangement in center of dorsal surface of head. Insert in lower right-hand corner shows outline of head and area detailed in sketches to show the several configurations (A-G). Solid dots indicate actual localities from which specimens were obtained, open circles placed in geographical center of a region indicate states from which specimens without more specific data have been recorded. Position of open circles consequently does not reflect actual collecting locality. See figures 26 and 28 for photographs of configurations A-G.

Pará and Pernambuco and southward through east-coastal Brazil to Santa Catarina and possibly Rio Grande do Sul; the pattern occupies the widest range and is seen in most of the available specimens. In pattern A the azygous scale is hexagonal, always broader than long, and thus, does not keep the prefrontals from

medial contact (cf. fig. 3A). The prefrontals may show variable longitudinal folding. Supraoculars are invariably present between the azygous and the oculars. The raphes between the azygous and the frontals or those between frontals are frequently absent, although this absence may be masked by folds.

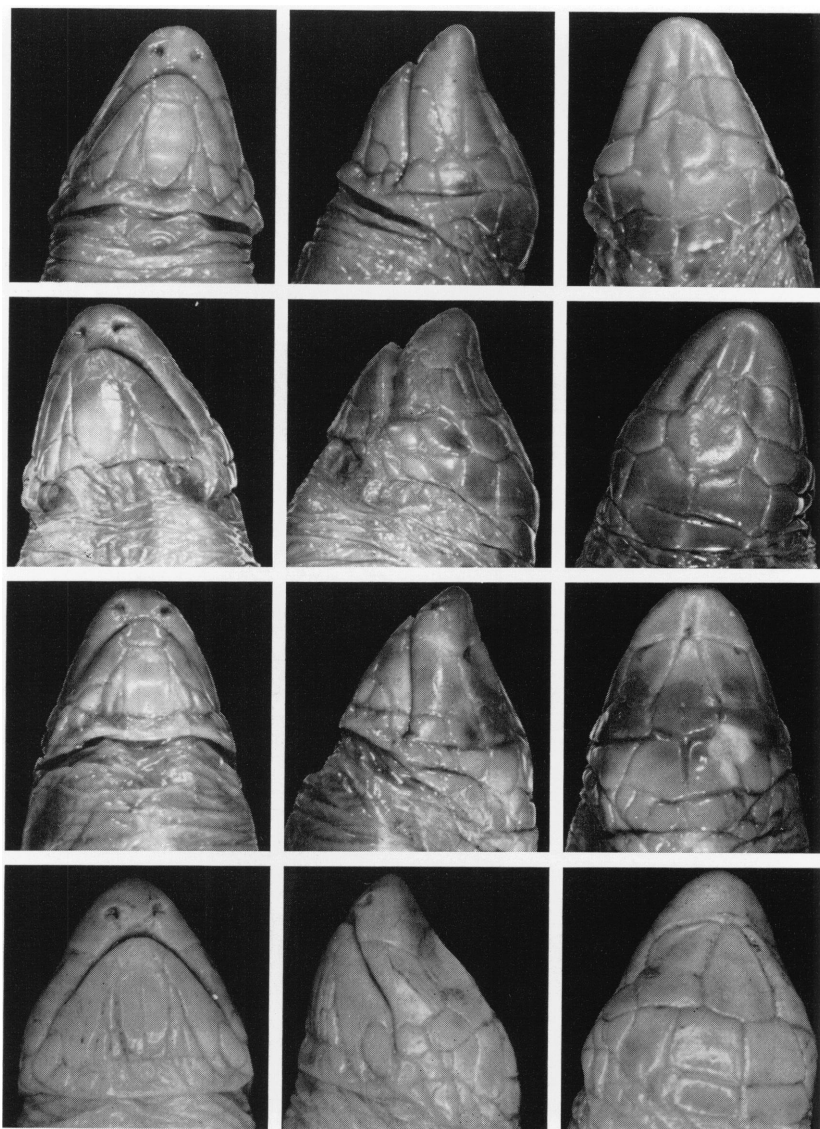


FIG. 26. *Leposternon microcephalum*. Ventral, lateral, and dorsal views of head. Top row: Configuration A, N.M.W. No. 33B, from Joinville, Santa Catarina, Brazil. Second row: Configuration B, N.M.W. No. 12368:4, from Joinville, Santa Catarina, Brazil. Third row: Configuration C, M.G. No. 1010.75, from "Rio Negro de Patagonia," Argentina. Bottom row: Configuration D, F.M.N.H. No. 66954, from vicinity of Fazenda Ipanema, Sao Paulo, Brazil.

In 43 per cent of the specimens from Santa Catarina and in those from Paraná, the azygous sends a narrow tip anteriorly to contact the rostronasal (configuration B, fig. 26). However, the body of the azygous remains hexagonal and the extension to the rostronasal begins abruptly near the medial tip to continue between the prefrontals to the rostronasal. The prefrontals of nearly all specimens from Santa Catarina are greatly folded. A few specimens of each of these two patterns have a complete raphe dividing either or both prefrontals longitudinally. Some specimens, again, lack the raphes between azygous and frontals (fig. 27).

The azygous scales of specimens from eastern Argentina and central Sao Paulo are narrow rather than broad. Most specimens from eastern Chaco, Corrientes, and Misiones, Argentina show a hexagonal azygous that is longer than broad (configuration C, fig. 26). In addition to being narrow, the azygous is also anteriorly elongate so that its tip reduces the length of the medial prefrontal suture or may even come into contact with the rostronasal. Two specimens from Fazenda Ipanema, Sao Paulo and the remaining ones from eastern Argentina lack a hexagonal azygous. In this pattern (configuration D, fig. 26) the azygous is in broad contact with the rostronasal. The anterior angles of the azygous are thus less distinct and the segment appears shield-shaped (fig. 5). Supraoculars occur in both patterns C and D. The prefrontals are neither furrowed nor folded but are reduced in size because of the central intrusion of the azygous. The raphe between azygous and frontals is rarely missing.

Specimens from Paraguay, and those from Formosa and central Chaco, Argentina lack supraocular scales. They thus seem to have only

four rows of dorsal segments. Two patterns occur, apparently in the same area. The first (configuration E, fig. 28) shows fusion of supraoculars and prefrontals but otherwise resembles configuration D. The contact of azygous and rostronasal may be very broad, almost the full width of the former. The second configuration F (fig. 28) shows nearly complete fusion of azygous, prefrontals, and supraoculars (fig. 6). Variable remnants of the raphe between these shields are seen in many cases.

Specimens from Bolivia, as well as those from adjacent Mato Grosso, Brazil, and Salta, Argentina have a characteristically small and narrow azygous (configuration G, fig. 28). This is roughly hexagonal, although the anterolateral corners may be rounded so that a shield-shaped dip extends anteriorly between the prefrontals (fig. 8). The prefrontals are never furrowed and all raphes are complete.

HEAD PATTERN—VENTRAL: The segmental arrangement of the chin shows marked geographical variation, particularly in the malar region (use figs. 26, 28, 29 as guides to the following discussion). Three questions may be asked. (1) Is the chin region long or short? (2) Is the region between the posterior edges of the infralabials occupied by the postmental and perhaps one pair of "malars" or is it filled with various small segments occupying the region posterior to the first infralabials? (3) Does a pair of enlarged postgenial or malar segments flank the postmental, and how far does contact extend anteriorly and posteriorly?

The specimens from Amazonas, Pará, Pernambuco, and the eastern coast of Brazil (configuration A) have an elongate chin region and very large first and tiny second infralabials. Medial to the latter lie two pairs of malars, the first small, the second extending anteriorly to embrace the posterior half of the large postmental. A small pair of segments in some cases lies at the angle between the second infralabial and the lateralmost malar.

Specimens from the western half of the range (Argentina, Bolivia, and Mato Grosso, Brazil, as well as a few from Paraguay) show a whole row of more or less large posterior segments crossing the chin between the second infralabials. Three pairs of enlarged malar segments lie on either side of the postmental, whereas two small postgenials lie posterior to this segment. The junction between second infralabial and lateralmost

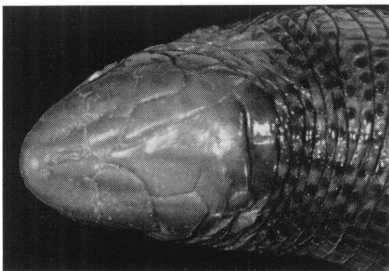


FIG. 27. *Leposternon microcephalum*. Dorsal view of head of N.M.W. No. 12368:5, from Joinville, Santa Catarina, Brazil, showing loss of cephalic sutures.

malar is again occupied by a small segment.

A fourth pair of malars lies anterior to the remaining ones (so that the smaller segments are arranged in two rows) between the postmental and first infralabial. Two configurations are noted. In specimens from eastern Chaco,

Misiones, Corrientes, and Entre Rios, Argentina, these anterior malars extend the entire length of the postmental, often reaching anterior point contact with the mental (configuration B). In specimens from the central Chaco, Formosa, and Salta, Argentina; Mato Grosso, Brazil; Bolivia

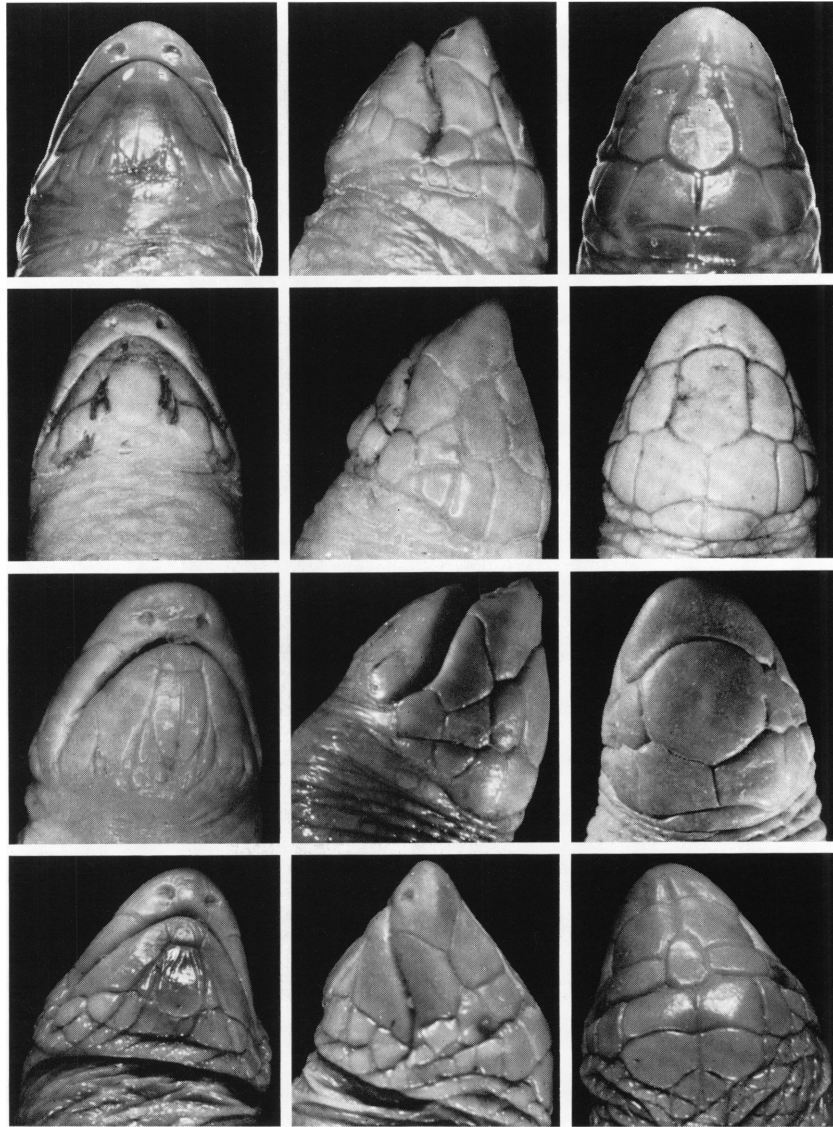


FIG. 28. *Leposternon microcephalum*. Ventral, lateral, and dorsal views of heads of specimens from Paraguay and Argentina. Top row: Configuration variant of C, Z.S.M. No. 231/33, from Apa-Bergland, Paraguay (characteristic of Paraguayan Group 1). Second row: Configuration E, N.M.B. No. 3819, no locality, Paraguay (characteristic of Paraguayan Group 2). Third row: Configuration F, B.M. No. 1958.1.2.10, from Primavera, Paraguay (characteristic of Paraguayan Group 3). Bottom row: Configuration G, M.A.C.N. No. 3217, from Buenavista, Santa Cruz, Bolivia.

and parts of Paraguay, the anterior malars extend only along the mid-portion of the postmental (configuration C).

Two specimens from Fazenda Ipanema, Sao Paulo, Brazil (configuration D) are similar to the

latter pattern except that their first infralabials have apparently fused with the lateralmost pair of malars so that they send back wings to the posterior edge of the chin plate.

Configuration C shows a number of variations

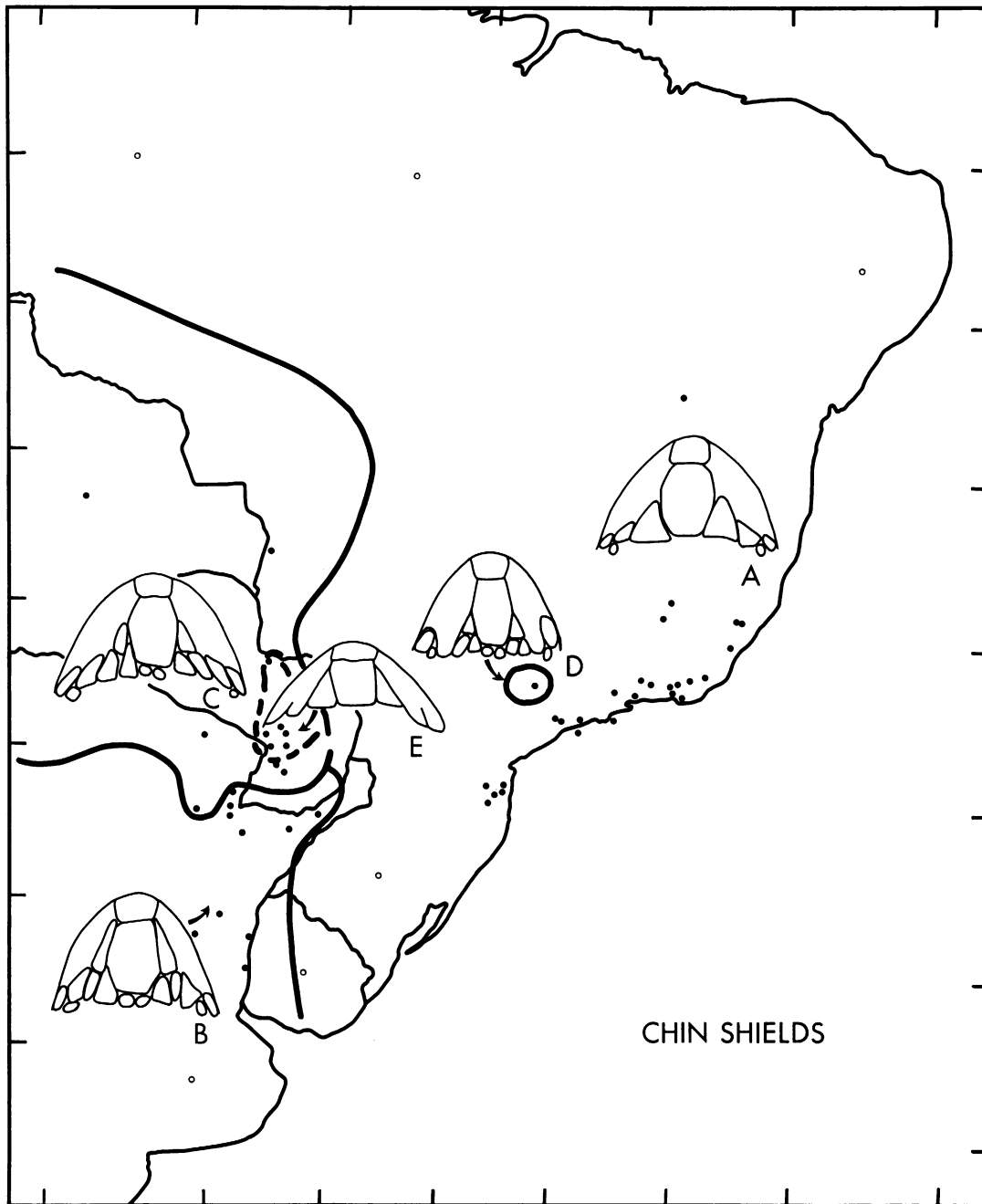


FIG. 29. *Leposternon microcephalum*. Distribution of the several variants (A-E) of ventral chin segmentation. All other details as in figure 25.

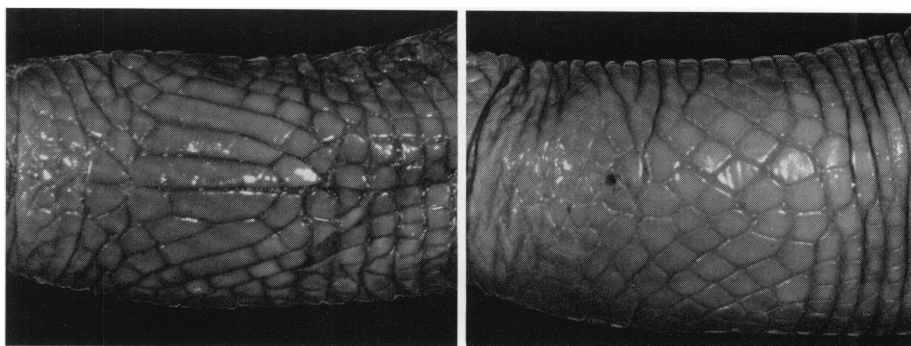


FIG. 30. *Leposternon microcephalum*. Pectoral patterns. Left: N.M.W. No. 12364:6, from Joinville, Santa Catarina, Brazil, showing "eastern" pattern. Right: U.M.M.Z. No. 60651, from Buenavista, Santa Cruz, Bolivia, showing "western" pattern.

in specimens from Paraguay leading to the extreme noted as configuration E, which is found in all specimens having the dorsal head configuration F (see fig. 29). The chin shield region is relatively short and expressed in a shortening of the postmental, which is still followed by two, more medial, postgenials. Lateral to the postmentals there is a single triangular postmalar on each side, but all the other segments, including the second infralabials, tend to be irregularly fused with the first infralabials although various remnants of raphes remain, in many cases unilaterally.

PECTORAL SEGMENTATION: The arrangement of segments in the pectoral region shows considerable individual variability. The general pattern is one of two medial rows of segments that parallel each other across the midline for at least the posterior portion of the region. The more lateral rows slant toward the medial ones giving the general impression of anteriorly open chevrons. It is possible to recognize two general arrangements (figs. 30, 31).

Specimens from Amazonas, Pará, Pernambuco, and the entire eastern coast of Brazil invariably show the segments of the medial row more or less completely fused, giving the impression of a pair of longitudinal shields. One to three rows may show partial fusion of segments either longitudinally or between adjacent rows. The chevron arrangement of segments tends to be maintained and the various segments appear enlarged, with straight sides and sharply angular corners.

Specimens from Mato Grosso, Brazil, from Bolivia, Paraguay, and Argentina show little or

no fusion of segments in the pectoral region. The medial rows are parallel posteriorly, but diverge anteriorly with the intersegmental space filled with small, usually rounded segments. The medial line is seldom distinct. The segments of the medial row may be large and angular but those of the more lateral rows tend to be smaller and rounded.

PIGMENT ARRANGEMENT: Nearly all specimens retaining pigmentation show countershading with a light yellow-brown to a darker brown dorsal surface. The main variability is noted in the distribution of pigmentation on each segment (fig. 32).

Specimens from Amazonas, Pará, Pernambuco, and southward through coastal Brazil show a characteristic concentration of pigmentation within a rounded zone in the center of each dorsal segment (fig. 33), giving the specimens a dotted appearance. The tail often shows several medial rows of darker segments and the pigmentation extends onto the ventral surface. The most posterior segments of the cephalic shields are usually pigmented evenly and more darkly than the remainder of the dorsal surface of the body.

Specimens from the state of Mato Grosso, Brazil, Paraguay, and Argentina have all segments of the dorsal surface pigmented fairly evenly with the pigmentation fading out gradually along the sides to produce countershading (fig. 33). The tail is usually darker than the body and a few specimens show denser pigmentation in the center of a few dorsal segments. The posterior head shields are almost always dark and evenly pigmented.

The most distinct coloration occurs in specimens from Bolivia and the state of Salta, Argentina (fig. 34). These specimens tend to be lightly countershaded, their pigmentation generally even. However, one or two rows of segments

ventral to the lateral sulci show very dark brown and centrally situated dots. These dotted rows occur so consistently in the samples that it is unlikely that they represent artifacts of selective fading. The tail of these specimens is in many

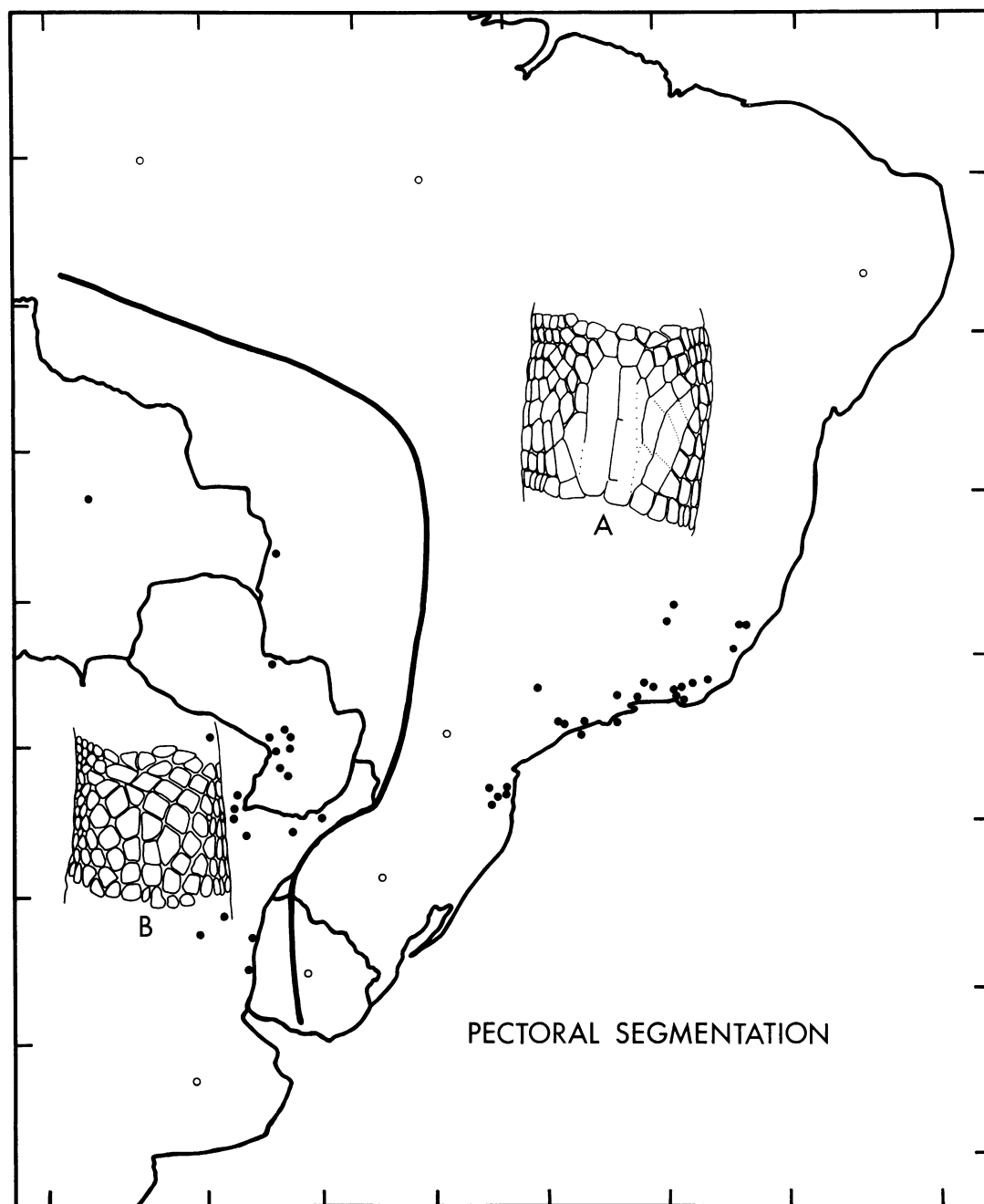


FIG. 31. *Leposternon microcephalum*. Distribution of the two variant conformations (A, B) of pectoral patterns. All other details as in figure 25. Compare the sketches with the photographs in figure 30.

cases darker than the body and occasionally has several middorsal rows of very densely pigmented, dark segments.

ANTERIOR LATERALS: Counts for anterior lateral annuli range from 10 to 17; sample means

($N > 2$) range from 12.1 to 15.8 (fig. 35). The samples from most of the range tend to have means ranging from 12.1 to 13.9. Higher means are seen in only two areas. In a coastal zone (in the vicinity of Guanabara and the cities of Rio

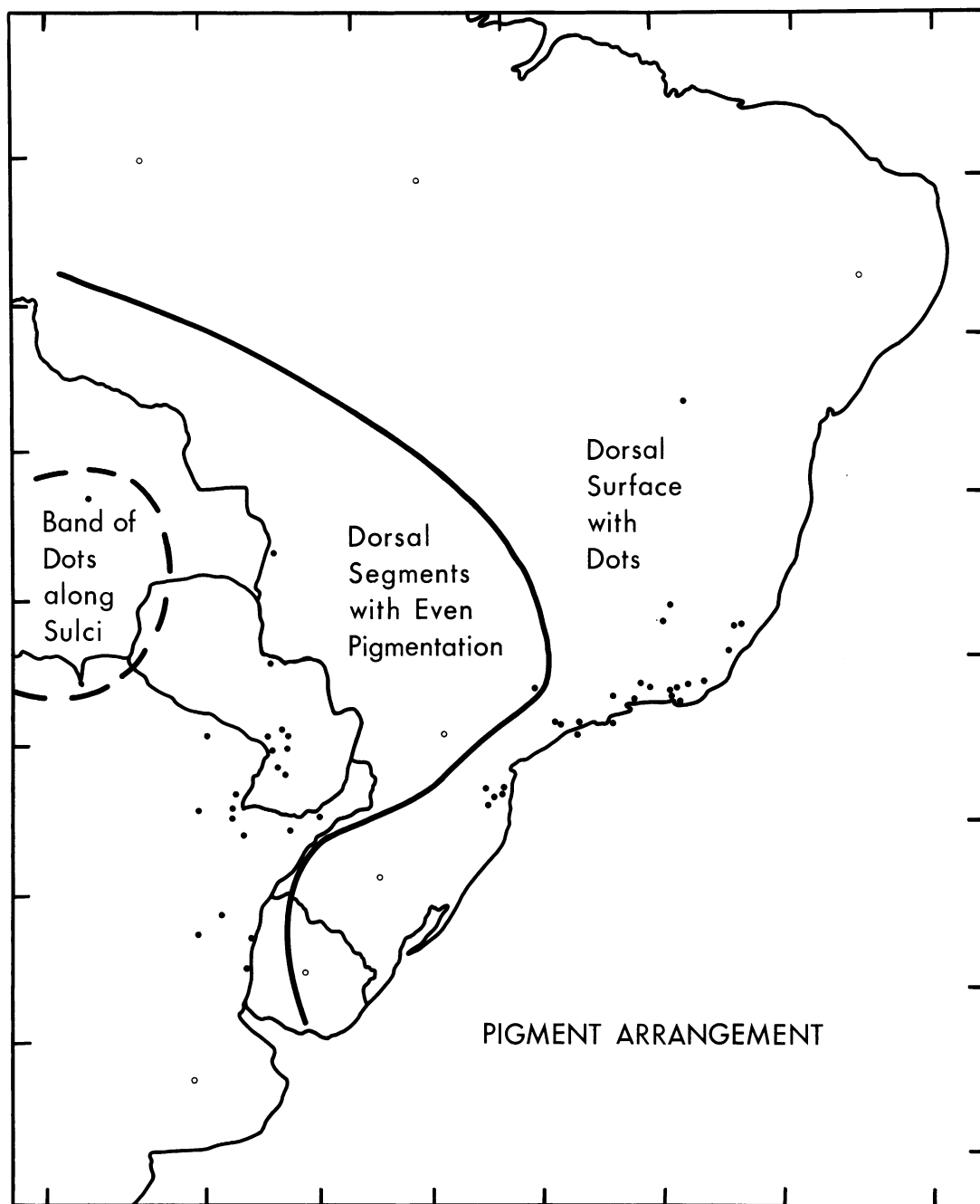


FIG. 32. *Leposternon microcephalum*. Map showing approximate distribution of the several color-pattern variants seen in this species. All other details as in figure 25. Compare with figures 33 and 34.

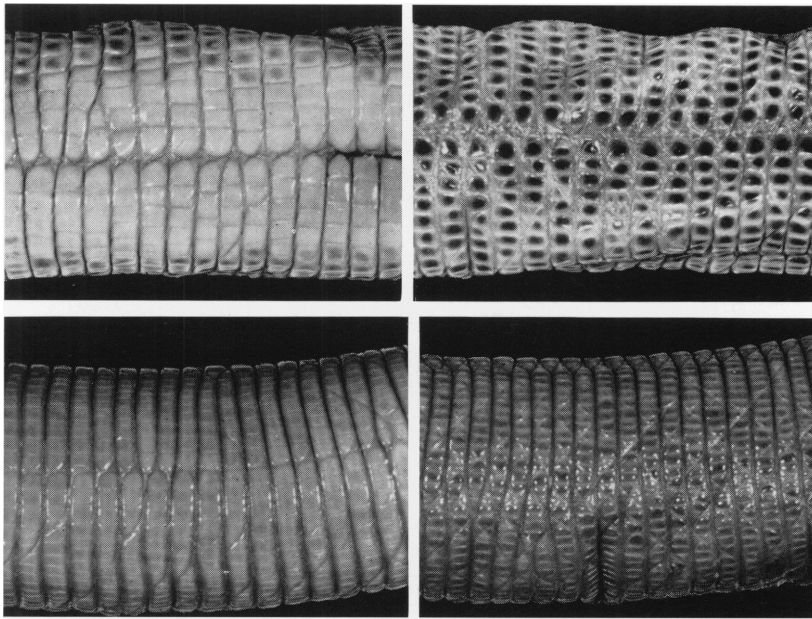


FIG. 33. *Leposternon microcephalum*. Midbody views. Top: Dorsal (right) and ventral views of N.M.W. No. 12368:5, from Joinville, Santa Catarina, Brazil. Bottom: Dorsal (right) and ventral views of B.M. No. 1958.1.2.10, from Primavera, Paraguay.

de Janeiro and Santos, Sao Paulo, as well as some of the intervening localities) they range from 14.2 to 14.6; in an inland assemblage of localities (Mato Grosso, Brazil; Bolivia; and Salta, Argentina) they range from 14.1 to 15.8.

POSTPECTORAL ANNULI—VENTRAL COUNT: The counts of ventral half-annuli in the postpectoral region are shown in figure 36. The vast majority of specimens exhibit values between 190 and 210, whereas most of the sample means fall between 195 and 205. An exception is formed by the series of three specimens from Urucum, Mato Grosso, Brazil, whose mean of 180 is low. In contrast, specimens from both inland and coastal localities in Sao Paulo appear to have somewhat higher values than do those comprising most of the remaining population.

The highest counts are found in central Paraguay and the adjacent portions of the state of Formosa in Argentina. The values there for individual specimens range from 221 to 277, whereas the sample means range from 239.1 to 255.1. Specimens from localities slightly farther south and east in Argentina show intermediate counts but the representation of sample localities is clearly insufficient for plotting isophenes.

Specimens from the two coastal islands agree with the counts obtained for individual samples from more northern and southern coastal localities. Their counts differ from those of specimens from the coastal region at Santos or from more inland portions of the state of Sao Paulo, off which these islands lie.

POSTPECTORAL ANNULI—DORSAL: When comparison proceeds on the basis of numbers of half-annuli along the dorsal rather than the ventral surface, an almost identical pattern is obtained, except that the values are generally higher. Most specimens show counts between 220 and 260. The excess of dorsal or ventral half-annuli is thus about 20 or more.

Populations found distinct in the previous discussion are generally also distinct when comparison is on the dorsal surface. Specimens from the center of Sao Paulo show slightly higher counts than those from surrounding areas, whereas the samples from Paraguay and from Formosa, and the adjacent Chaco in Argentina are again among the highest. The specimens from Urucum (Mato Grosso) do not differ significantly from those from adjacent Bolivia, whereas the specimen from the coastal island of Ilha

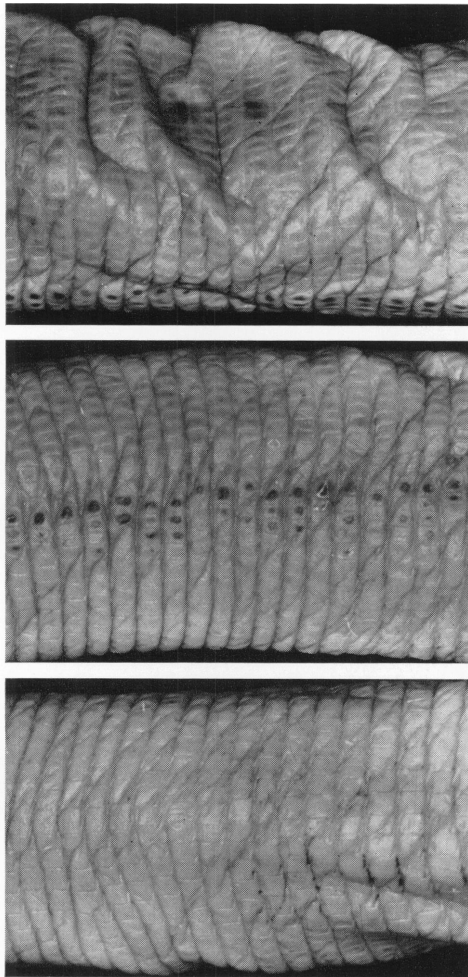


FIG. 34. *Leposternon microcephalum*. Dorsal (top), lateral, and ventral views of midbody of B.M. No. 1927.8.165, from Buenavista, Santa Cruz, Bolivia.

da São Sebastião agrees with values obtained on the adjacent mainland.

ACCESSORY DORSAL HALF-ANNULI: The differences noted in the pattern of dorsal and ventral counts of body annuli suggested that the differences be diagrammed. Some interesting trends appear. In most samples, the difference tends to range between 11 and 30 with means varying from 18.8 (generally over 20) to 27. Northernmost specimens (Pará, Amazonas, Bahia) seem to have slightly lower values than southern ones, but the difference is not significant. A drastically different pattern is seen in the specimens from Mato Grosso. Here the number of accessory dorsal half-annuli varies from 40 to 66; the

sample from Urucum has a mean of 56.3. Similar high values are found in specimens from the eastern Chaco, Argentina, although the intermediate samples from Paraguay, and indeed other Argentine samples, tend to be somewhat lower.

CAUDAL ANNULI: Figure 37 shows the distribution of caudal annuli. The number of these varies between 8 and 13 with most specimens having counts between 10 and 12. Most sample means fall between 10.4 and 11.5. One exception occurs in that the samples of southeastern Bolivia and the adjacent portions of Mato Grosso have means ranging from 8.3 to 9.5. The sample from Primavera, Paraguay, has a mean of 12.1, the highest for the species. No other trends are apparent.

NUMBER OF BODY VERTEBRAE: Figure 38 shows the numbers of body vertebrae. The counts for the available specimens generally fall into two groups that show almost no overlap. The majority of specimens, including all records from the eastern portion of Brazil, generally have counts ranging from 93 to 104. Only a single specimen from eastern Argentina shows a value of 91, whereas a few individuals from along the coastal region show values of 103 and 104. Sample means generally range between 90 and 101.

The specimens from extreme northern Salta, Argentina, from Bolivia, and from western Mato Grosso, Brazil, have counts ranging from 82 to 91, whereas their sample means range from 84.1 to 89.1. They consequently show almost complete non-overlap with specimens from other regions. This is noted particularly in figure 39, which also documents the fact that the number of dermal annuli varies independently of the vertebral number.

NUMBER OF SEGMENTS PER ANNULUS: Figures 41 and 42 present the geographical variation for numbers of segments respectively to a dorsal or a ventral half-annulus. The ranges of individual specimens are given as before and means ($N > 2$) are written as those separated by a line. All values are given to the first decimal point as the segmental numbers are themselves means of multiple counts (see Characters).

The pattern for dorsal segments exhibits a remarkably clear dichotomy. Specimens from Mato Grosso, Bolivia, Paraguay, and Argentina invariably have sample means above 24 and generally above 26. In contrast, samples from

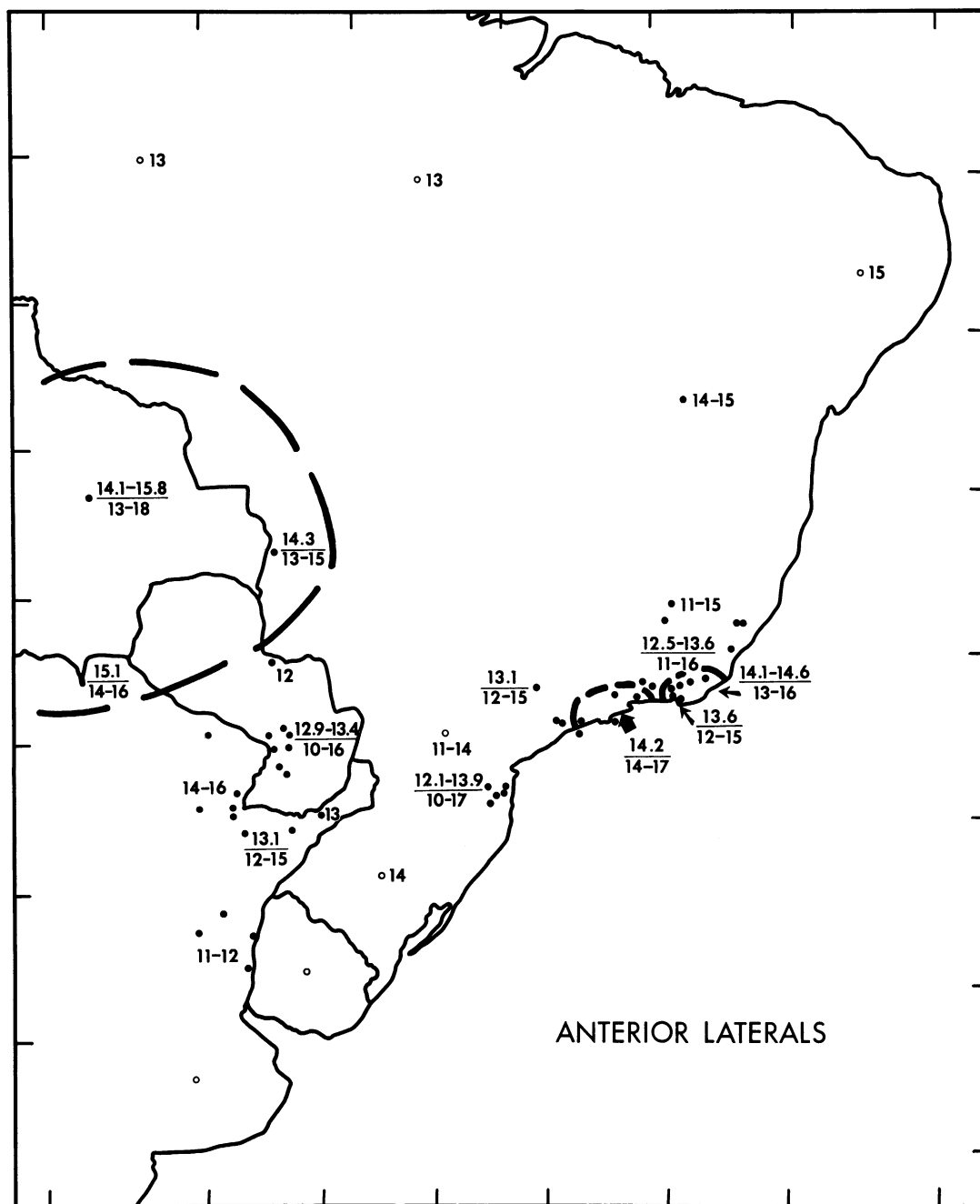


FIG. 35. *Leposternon microcephalum*. Map showing approximate distribution of the numbers of anterior lateral annuli. A single value or a range indicates that less than three specimens were available from each of the localities included. When the samples were larger ($N > 2$), values above the line give the distribution of sample means whereas those below indicate the range of individual values. All other details as in figure 25.

the more eastern portion of the range tend to have sample means from 18.1 to 24.7. The ranges for individual counts go from 23.6 to 33.0, and those from coastal specimens go from 17.2

to 26. Samples from the northern portion of the range (Minas Gerais to Pará and Amazonas) show clearly lower values than do samples from Rio de Janeiro to Santa Catarina.

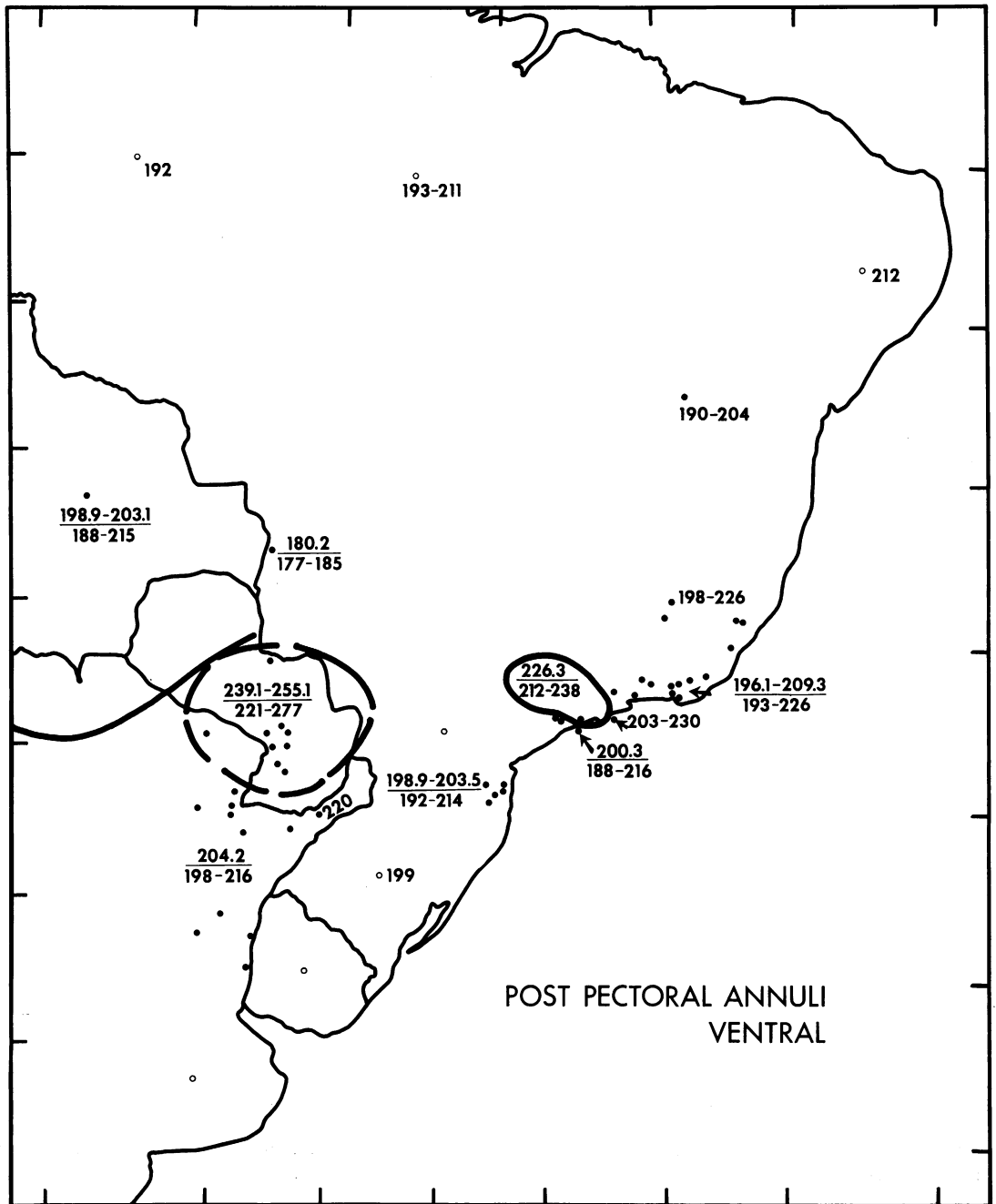


FIG. 36. *Leposternon microcephalum*. Sketch map showing distribution of numbers of postpectoral half-annuli counted along the ventral surface. All conventions as in figures 25 and 35.

Means for the western assemblage are from (26.9 in southern Argentina) 29.1 to 38.1 with individual counts ranging from 21.0 to 43.2. Means on the eastern assemblage are from 20.3

to 25.0 with individual counts ranging from 18.6 to 32.0.

BODY PROPORTIONS: The maximum snout-vent length shows some marked differences, the

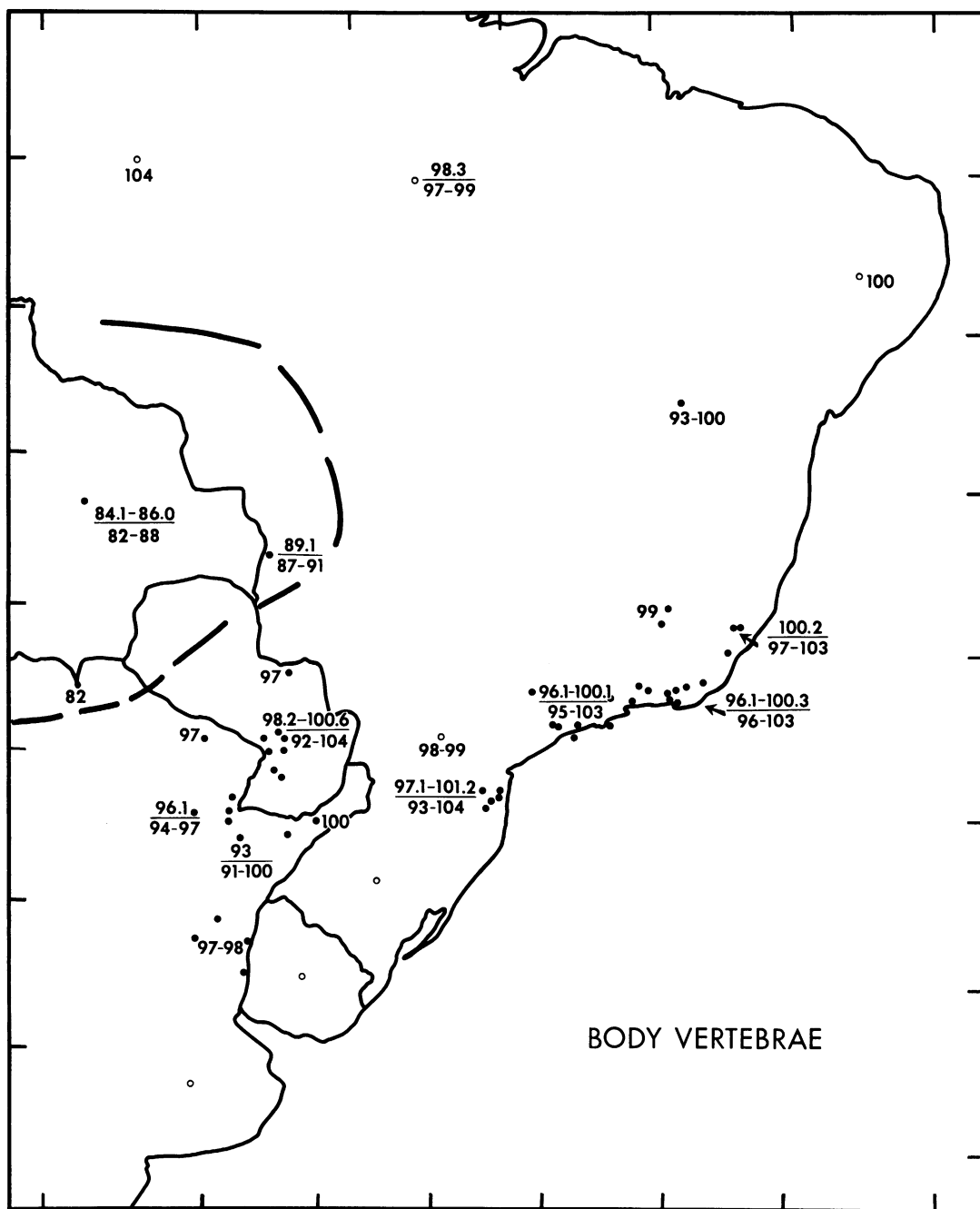


FIG. 38. *Leposternon microcephalum*. Sketch map showing distribution of body vertebrae (counted from head joint to cloacal region) for the available samples. All conventions as in figures 25 and 35.

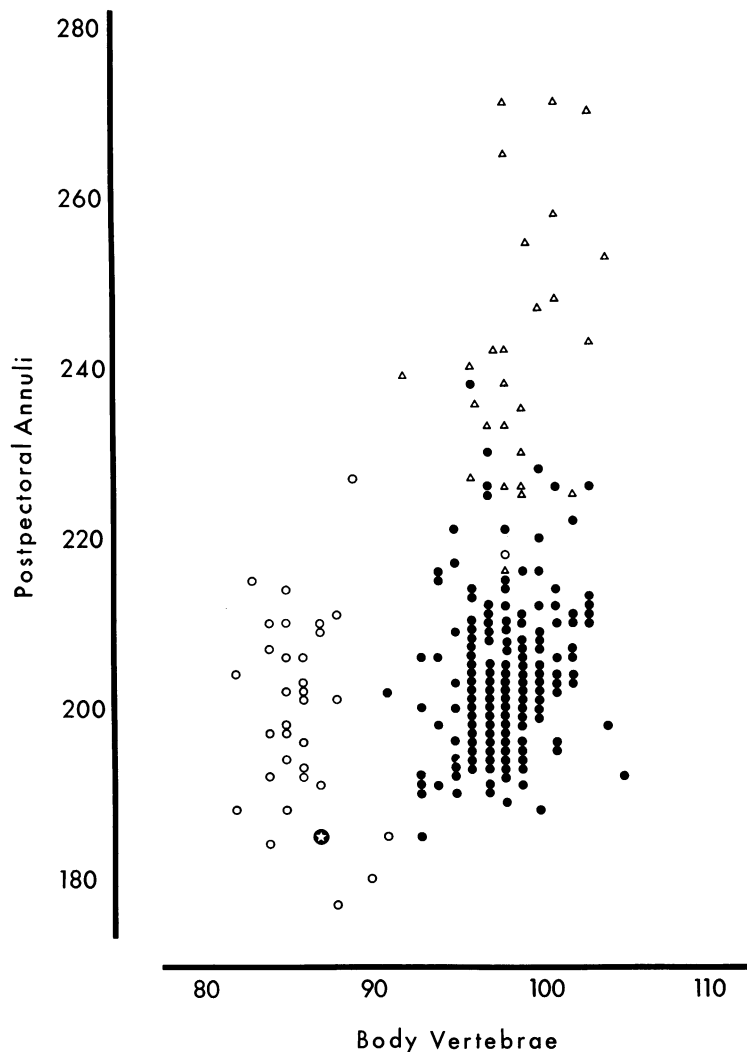


FIG. 39. *Leposternon microcephalum*. Scatter diagram comparing number of postpectoral annuli to number of body vertebrae for the available specimens. Open circles indicate specimens from Bolivia, northern Salta (Argentina), and Mato Grosso; triangles, specimens from Paraguay; and solid dots, those from the remainder of the range. The open star refers to holotype of *L. phocaena* whose type locality "Buenos Ayres" is here restricted to "Bolivia."

significance of which is unclear because of the relatively small sample size. The largest specimens pertain to the sample from Rio de Janeiro with the specimens from Sao Paulo and Santa Catarina being slightly smaller. Inspection of the limited records from Paraná, Minas Gerais, Espírito Santo, and Bahia suggests that they all appear to have been sampled from a population of large specimens. In contrast, specimens from

Pernambuco, Pará, Mato Grosso, and Amazonas, Brazil, as well as those from Paraguay, Bolivia, and Argentina show both the lower maximum values and generally the lower modal values as well (fig. 42).

There is some obvious variation in relative midbody diameter but the present samples are inadequate to say more than that the specimens from Bolivia plus a few from Paraguay,

Argentina, and Mato Grosso tend to have a wider midbody diameter than do those from east coastal localities (fig. 43).

The relative tail length shows further slight differences. Specimens from the coastal regions

between Santa Catarina and Pará do not show significant differences, whereas those from Mato Grosso, Bolivia, Paraguay and Argentina seem to have slightly shorter tails (fig. 44).

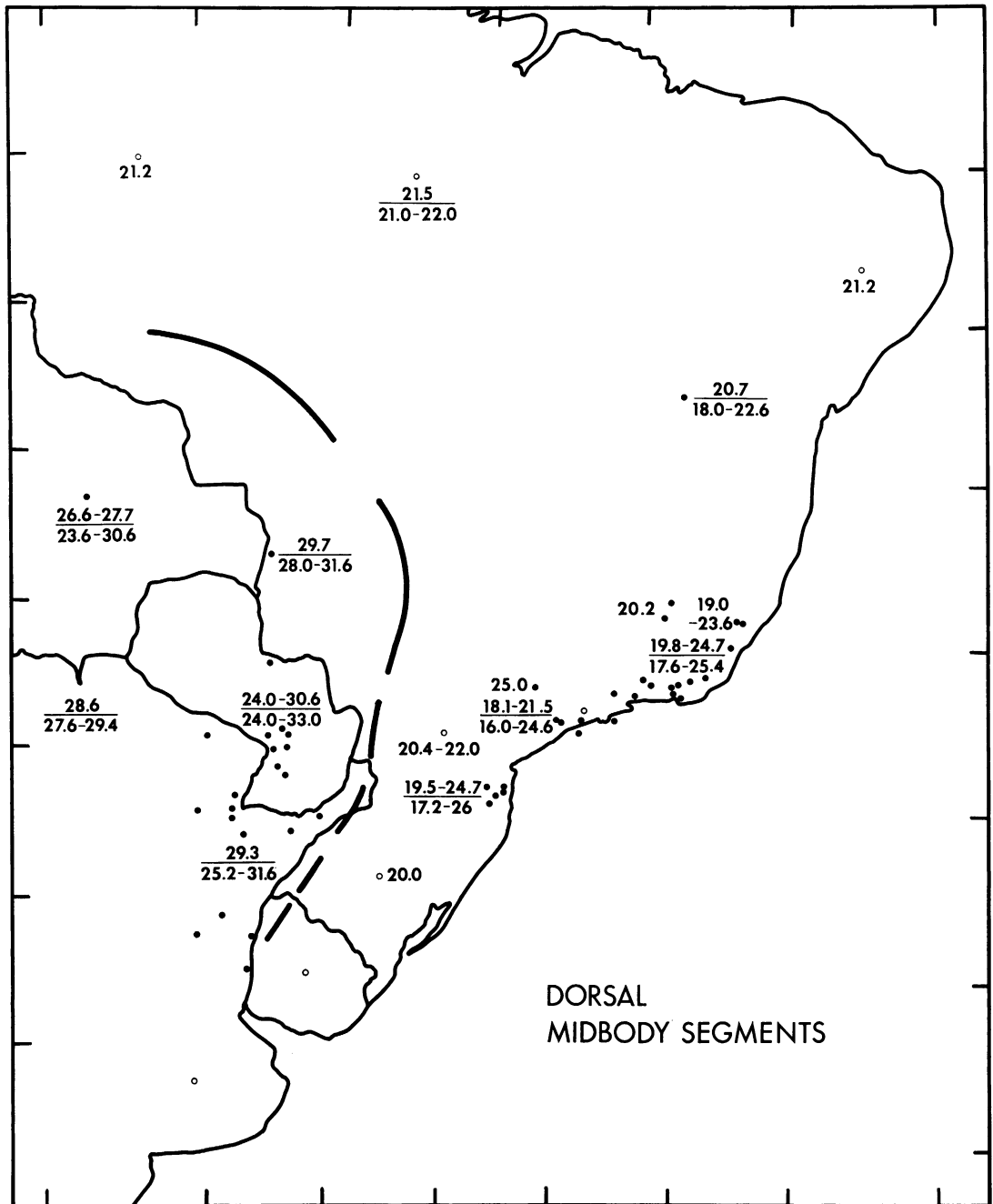


FIG. 40. *Leposternon microcephalum*. Sketch map showing distribution pattern for mean numbers of segments to a dorsal half-annulus. All conventions as in figures 25 and 35.

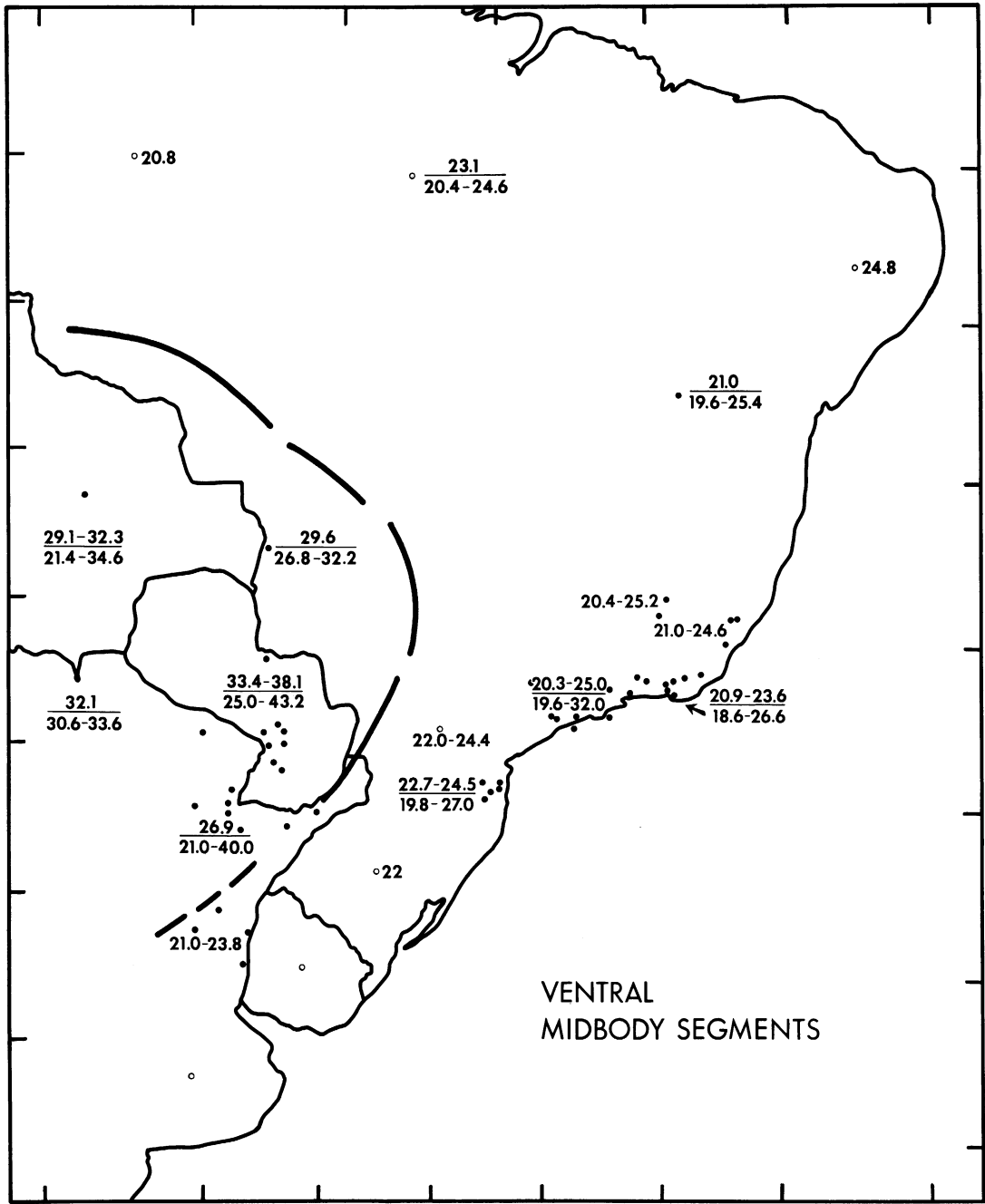


FIG. 41. *Leposternon microcephalum*. Sketch map showing distribution pattern for mean numbers of segments to a ventral half-annulus. All conventions as in figures 25 and 35.

SUMMARY OF VARIATION

Certain general trends become apparent when the separate patterns are summarized. Sharp differences are seen in particular characters, and

the lines along which these occur often agree between characters or are parallel but displaced. Many of the sharp differences occur across areas in which there are relatively few samples so that

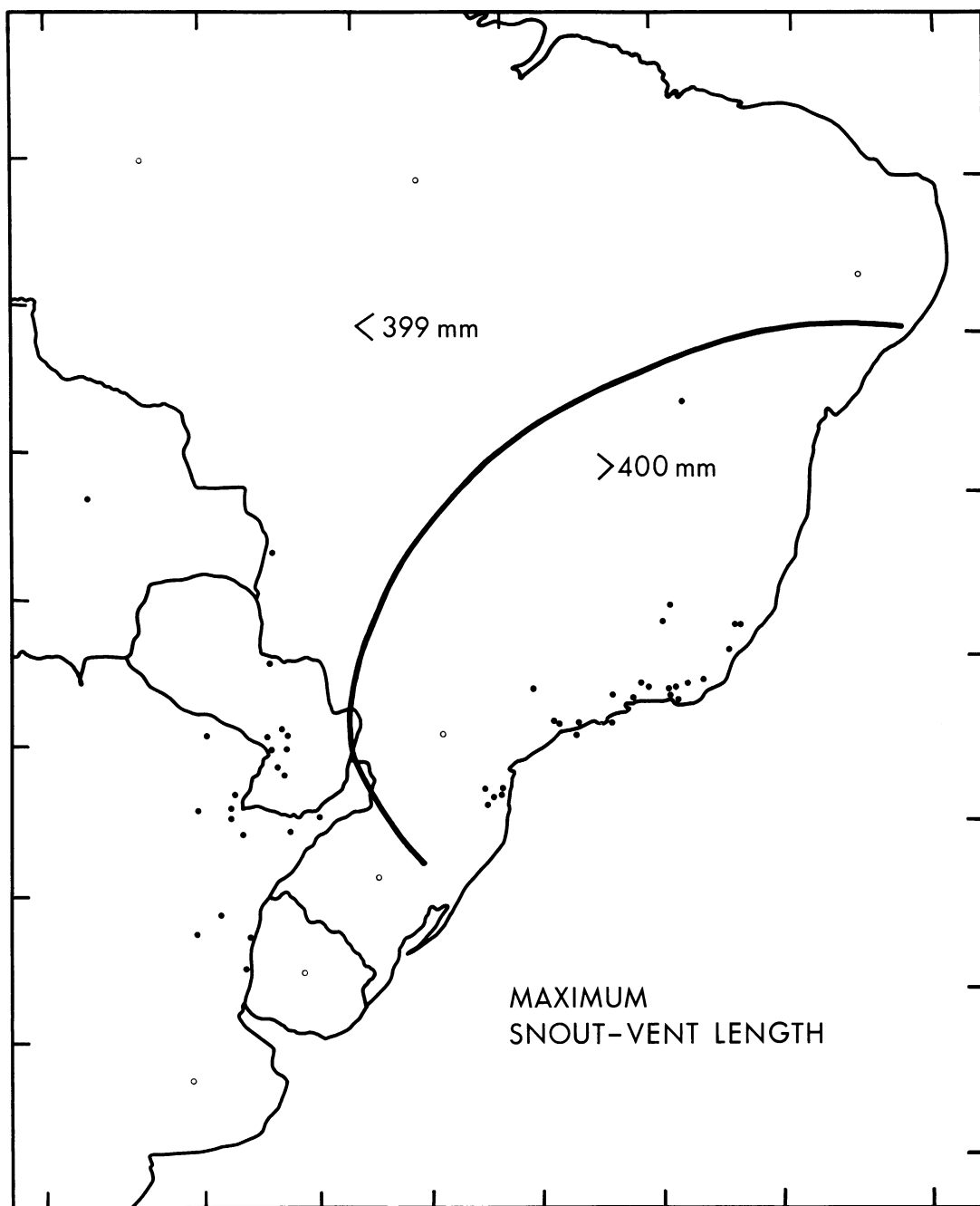


FIG. 42. *Leposternon microcephalum*. Sketch map showing ranges occupied respectively by "adult" specimens with snout-vent length of less than 399 mm. and of snout-vent length of more than 400 and up to 600 mm. All conventions as in figure 25.

it is uncertain whether structurally intermediate specimens would occur in the geographically intermediate zone. Yet certain other characteristics of the population do not vary in parallel.

However, the difference between two populations generally increases as one proceeds along any transect. The present assemblage presumably represents a single species including

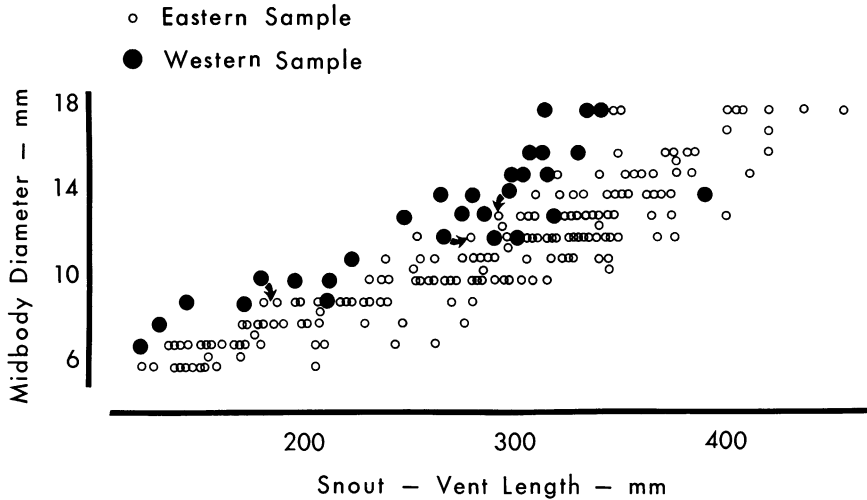


FIG. 43. *Leposternon microcephalum*. Scatter diagram showing relative midbody diameter versus snout-vent length for the sample from Santa Catarina compared to the composite sample from Bolivia and Mato Grosso, which areas are typical respectively for the eastern and western groupings.

considerable individual and geographical variation.

Within the species, we can recognize a population extending from northeastern Brazil along the coast to Santa Catarina, a distinct population occupying Bolivia, adjacent Mato Grosso, and northern Argentina, and a population occupying central Paraguay and adjacent Argentina. Certain populations from coastal Rio de Janeiro and Sao Paulo seem distinct, but the sample size is inadequate to characterize them.

The sample from Bolivia differs from all other samples in the number of anterior laterals, in the number of caudal annuli, and in the low numbers of body vertebrae. The assemblage is also characterized by a unique arrangement of cephalic shields, by an unusual and characteristic pigment arrangement, and by body proportions. Their skin segmentation is also suggestive of differences, as is their absolute size and numbers of dorsal and ventral segments to a midbody annulus, although these characteristics are, to some extent, shared with specimens from Paraguay and more central Argentina.

The samples from central Paraguay exhibit several unique segmental arrangements on both the dorsal and ventral surfaces of the head. Although the segmentation pattern within this general area is remarkably diverse, it shows local constancy (fig. 7). These samples also show

markedly high numbers of postpectoral half-annuli both on the dorsal and ventral surfaces of the body. On the other hand, the vertebral counts of this group do not appear to be significantly different from those of specimens from the Brazilian coastal region. We thus see a multiplication in the number of body annuli rather than in the number of vertebrae.

Samples from northeastern Argentina are similar to variants of the Paraguayan samples. In characteristics such as number of postpectoral annuli they show some degree of intermediacy between the former and specimens from the Brazilian coast, but they agree with Paraguayan rather than Brazilian specimens in their pigmentation.

The several large samples from the coastal region of Brazil are then seen to differ in various ways from the samples above described. Yet the several coastal samples also show local variability and it is already possible to predict the source of individuals and small samples.

The general pattern indicates that this species seems to be distributed across a U-shaped range, passing from Bolivia, to Paraguay and Argentina, and across Santa Catarina, north along the coast of Brazil to Pará.

Leposternon octostegum

A single specimen (M.H.N.P. No. 7055),

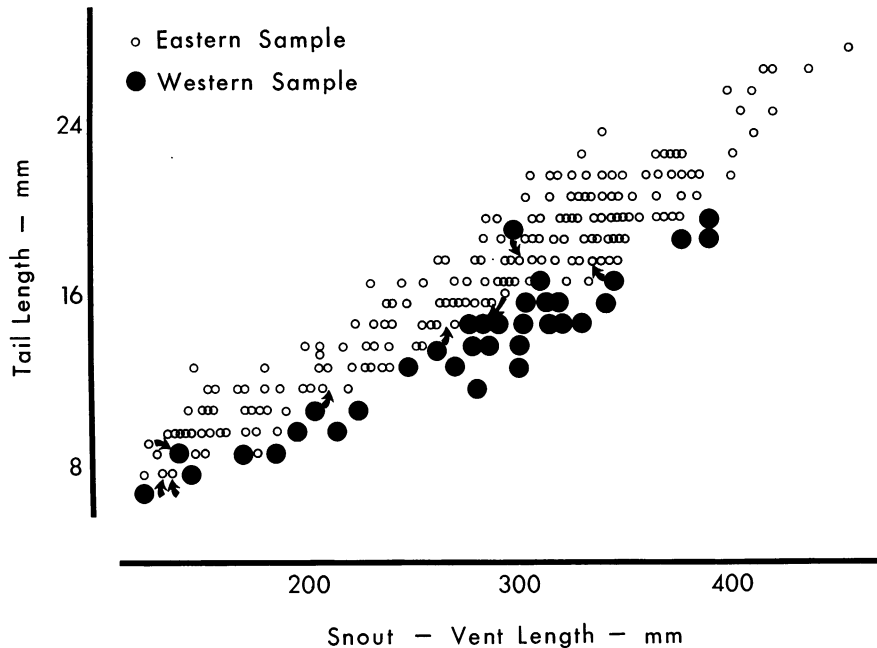


FIG. 44. *Leposternon microcephalum*. Scatter diagram showing relative tail length versus snout-vent length for sample from Santa Catarina and compared to a composite sample from Bolivia, Salta, Western Paraguay, and Mato Grosso, which are typical respectively for the eastern and western groupings.

lacking data, could not be assigned to any of the previously characterized groupings. Its difference from these is extreme and involves the arrangement of cephalic and pectoral segments (figs. 45, 46), and a high number of postpectoral annuli (378) coupled with a relatively low number of body vertebrae (106).

It is possible that the individual represents a geographical variant of any of the characterized species from an area not otherwise sampled. This is unlikely as the character states of the specimen are so diverse that it is not even possible to guess at its affinities. There is also Strauch's (1881) report of a second specimen (now lost, but once in the Bonn Museum and from "Bahia"), sharing both shield geometry and high numbers (362) of postpectoral annuli. The form is hence retained as a valid species.

SUPPLEMENTARY CHARACTERS

GENERAL: The preceding analysis has demonstrated the existence of at least six species in the genus *Leposternon*. The taxonomic decisions were made on the basis of the few characters that provided sharp discrimination by the presence or

absence of character states or their non-overlap if meristic. The limited number of specimens having accurate locality data eliminated certain other characteristics from consideration. Yet other differences do exist between species and may be briefly noted.

PRECLOACAL CAPS: Although a significant number of specimens show irregular subdivisions of the segments on the posteriorly rounded precloacal cap, it is possible to characterize the following species patterns (figs. 47-49).

Leposternon scutigerum. The cap is generally subdivided into eight segments by straight raphes running parallel to the midline.

Leposternon polystegum. The cap is very irregularly subdivided, usually with two rows of segments, the raphe between the rows being a curve, more or less concentric with the posterior edge of the cap.

Leposternon wuchereri. The cap is subdivided into four to eight, generally six segments by radial raphes. Two narrow, elongate, transversely arranged segments lie between the cap proper and the last postpectoral annulus.

Leposternon infraorbitale. The cap is subdivided into three to four rows of segments, the raphes between

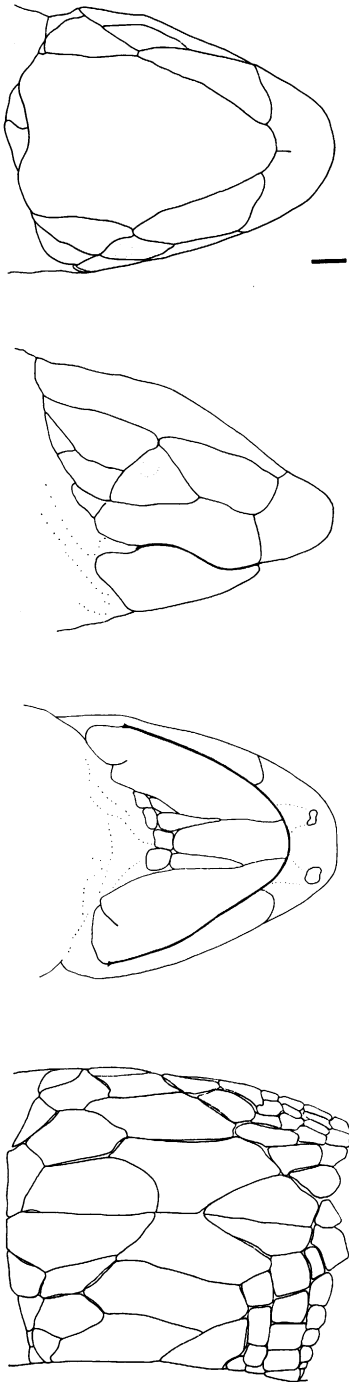


FIG. 45. *Leposternon octostegum*. Pattern of head scalation. Dorsal, lateral, and ventral views, and pectoral scalation of the holotype M.H.N.P. No. 7055, from Brazil. Dotted lines indicate areas of folding. Line equals 1 mm. to scale.

them curving concentrically so that the posteriormost row, comprised of very short and wide segments, runs from edge to edge while the anteriormost row is short and restricted to the center of the shield. The second and third rows appear to have the largest segments. Only the specimens from Barra do Tapirape have a simpler arrangement of radial segments.

Leposternon microcephalum (fig. 49). The precloacal shield of this species is quite variable. There are six to eight, radially and often somewhat asymmetrically divided segments. Additional secondary subdivisions are common. No particular geographical pattern could be noted.

Leposternon octostegum. The unique specimen has a narrow, elongate precloacal cap with a continuous posterior row of four large segments and a second, central concentrically separated row of four much smaller ones. This cap is more sharply curved but the pattern is otherwise intermediate between those of *L. polystegum* and *L. wuchereri*.

FUSION OF CAUDAL ANNULI: Certain specimens show irregularities of caudal annuli, most commonly a fusion of two or more dorsal into a single ventral quarter annulus. This characteristic is never seen in *L. octostegum* and *L. wuchereri* and rarely in *L. polystegum* and *L. scutigerum*. However, eight of 12 specimens of *L. infraorbitale* have either one, two, or three such fused annuli. Approximately 10 per cent of the overall sample of *L. microcephalum* also show this characteristic. Although the frequency of this characteristic is relatively low in most localities, it reaches approximately 30 per cent in specimens from Paraguay.

ABSOLUTE SIZE: Figure 50 presents histograms of snout-vent length for all samples. As noted in earlier papers, and indeed characteristic for reptiles as a group, the modal frequency is not at or near the largest size class but rather several classes below. This relative scarcity of individuals expected in the largest size class indicates that maximum size should only be compared for large-sized samples; these are, of course, not available for most of the present forms. Modal class may be a more important category.

The figure suggests that *L. infraorbitale* not only reaches the largest absolute size but appears to have a significant fraction of the population in a size grouping occupied by less than 10 per cent of the specimens of *L. microcephalum*. *Leposternon wuchereri*, *L. octostegum*, and the form from Arag  as show no evidence of differing from the values noted for *L. microcephalum*. In contrast,

specimens of *L. scutigerum* appear to be significantly longer than *L. microcephalum* although perhaps not so long as *L. infraorbitale*.

RELATIVE MIDBODY DIAMETER: It has already been noted that specimens from Bolivia, from adjacent Mato Grosso, from northwestern Argentina, and one or two from "Paraguay" have significantly wider midbody diameters for a given snout-vent length than do specimens of *L.*

microcephalum from more eastern regions. When a comparison with the good sample of *L. microcephalum* from Santa Catarina (fig. 51) is made, it may be seen that *L. wuchereri*, *L. polystegum*, and particularly *L. scutigerum* and *L. octostegum* are somewhat more slender. Several of the samples, particularly those of *L. polystegum* show considerable variability that cannot at present be assigned to sex or geography. Most of the specimens

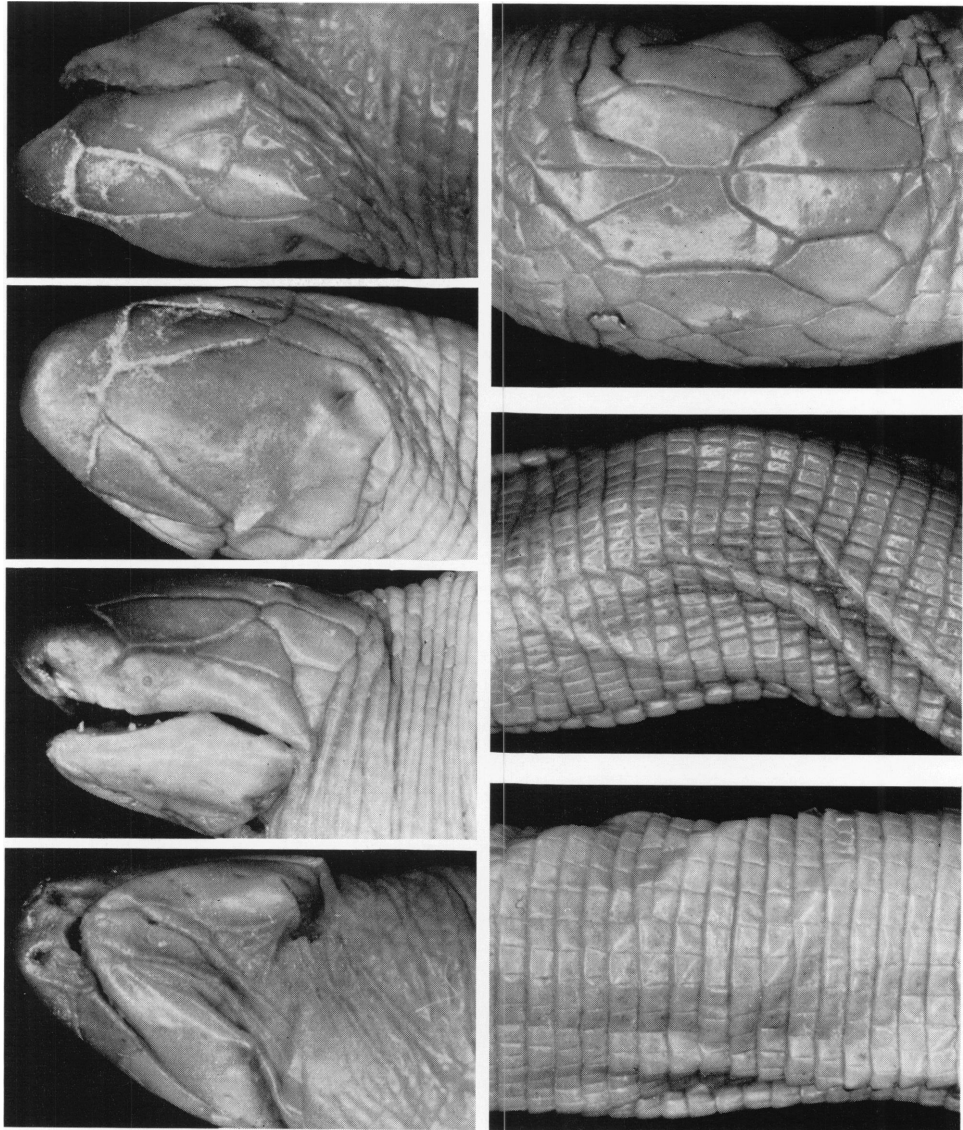


FIG. 46. *Leposternon octostegum*. Views of the holotype, M.H.N.P. No. 7055, from Brazil. Left column: Right lateral, dorsal, left lateral, and ventral views of head. Right column: Pectoral (top), dorsal, and ventral midbody views.

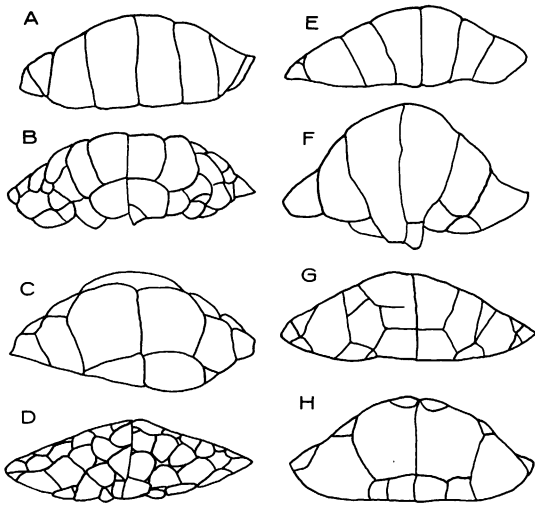


FIG. 47. *Leposternon*. Sketches to show typical patterns of prelocaal segments. A. *L. scutigerum*, H.M. No. 1684, no locality. B. *L. polystegum*, U.S.N.M. No. 58348, from Pernambuco, Brazil. C. *L. wuchereri*, C.G. No. 3721, from Espirito Santo, Brazil. D. *L. infraorbitale*, G.U.M. (unnumbered) from Bahia, Brazil. E. *L. microcephalum*, B.M. No. 26.3.16.12, from Rio das Velhas, north of Belo Horizonte, Minas Gerais, Brazil. F. *L. microcephalum*, M.A.C.N. No. 4407, from Salta, Argentina. G. *L. microcephalum*, N.M.W. No. 12369:1, from Joinville, Santa Catarina, Brazil. H. *L. octostegum*, M.H.N.P. No. 7055, from Brazil.

of *L. infraorbitale* have a relatively greater midbody diameter than do specimens of *L. microcephalum* from Santa Catarina but this seems to be apparent mainly in the size region above 400 mm. Thus the slope of the estimated regression line is greater and the y intercepts less than in *L. microcephalum*. As the size of the specimen from Aragarças falls within the modal class sample of the *L. microcephalum* and below 400 mm., there are no significant differences.

RELATIVE CAUDAL LENGTH: The tail is relatively short (not more than twice the diameter) and curves ventrad. As its distal tip is bluntly rounded, it is difficult to measure even to an accuracy of 1 mm. The resulting 5 to 10 per cent error complicates comparisons of individual specimens. The relative tail length of *L. scutigerum* does not differ significantly from that of the Santa Catarina sample of *L. microcephalum*. Specimens of *L. polystegum* and *L. octostegum* (fig. 52) appear to have a slightly smaller tail length even than that of the specimen of *L.*

microcephalum from Bolivia. The sample of *L. wuchereri* suggests that it differs, but the sample size is too small to permit decisions on this. The regression line for *L. infraorbitale* appears to be significantly different from that for *L. microcephalum* from Santa Catarina both in slope and y intercept; the two regression lines cross each other near 400 mm. so that specimens of *L. infraorbitale* smaller than this size have a relatively shorter tail length, and those larger, a much greater one.

SUMMARY AND DISCUSSION

The preceding analysis suggests that the genus *Leposternon* contains six species with a most curious distribution pattern. It is now possible to discuss the various ranges and at the same time to discuss their similarity to those of species of the widely sympatric genus *Amphisbaena*. The range of the genus *Leposternon* appears to be almost entirely defined by the range of the species *L. microcephalum*, which extends from Pará possibly inland on the right bank of the Amazon, south from Pará along the coast of Brazil to Santa Catarina, thence inland across Rio Grande do Sul into the northeastern states of Argentina and across Paraguay to the Argentine state of Salta. From here the species extends northward into Bolivia and adjacent Mato Grosso. There appears to be a hiatus in the range of this species between western Mato Grosso and the coastal states of Brazil.

The range of *L. microcephalum* thus partly overlaps the ranges of the widely distributed *Amphisbaena alba*, *A. fuliginosa*, *A. vermicularis*, *A. pretrei*, *A. mertensi*, *A. darwini*, and *A. prunicolor*. In no case is there significant concordance between the ranges, which suggests that the ecological association inhabited by *L. microcephalum* is likely to be different from that of any of the above species. The range of *L. microcephalum* wholly overlaps the more limited ranges of various species, such as *A. mitchelli*, *A. leucocephala*, *A. heathi*, *A. carvalhoi*, *A. bahiana*, *A. nigricauda*, *A. dubia*, and *A. roberti*.

The range of *Leposternon microcephalum* appears to be overlapped by the range of the more slender species *L. polystegum* extending from Pará inland to Rio Grande do Norte and Pernambuco and south to Bahia where it may be replaced by *L. octostegum* (of relative diameter equal to that of *L. microcephalum*), thus far known

from only two specimens. The distribution of these forms thus recalls those of *Amphisbaena pretrei* and *A. leucocephala*; in both cases, a fairly wide-ranging species of the northern bulge of Brazil is replaced by a quite similar but distinct species occurring within the state of Bahia. The ecological implications of this situation certainly deserve attention.

The fourth, quite distinct and again more slender species, *L. wuchereri*, occurs in a relatively restricted area from Bahia south to Rio de

Janeiro. Even though the azygous of *L. polystegum* tends to become extremely small in the northern Bahian population, the azygous of *L. wuchereri* is relatively large and significantly wider than long; consequently there is almost no similarity between the head scale arrangements of these two allopatric, but replacing, species. The supposed range of *L. wuchereri* includes the locality from which *Amphisbaena nigricauda* was described; both have apparently been taken at the same locality.

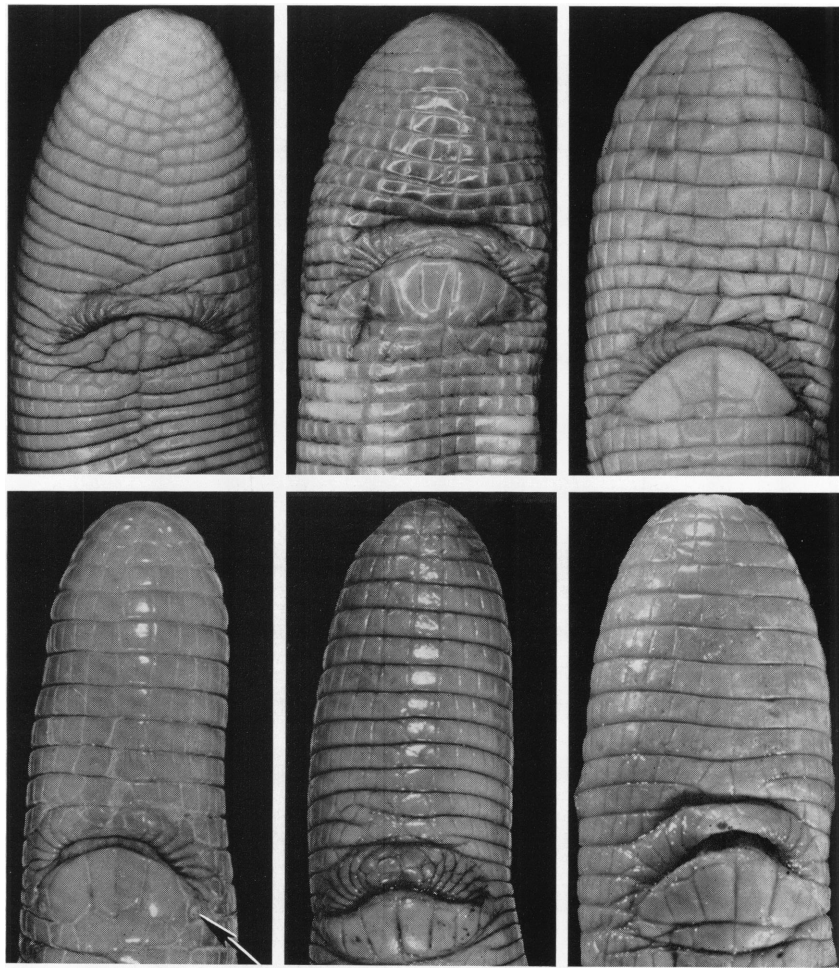


FIG. 48. *Leposternon*. Ventral views of cloaca and tail. Top row, left to right: *L. infraorbitale*, G.U.M. (unnumbered), from Bahia, Brazil; *L. infraorbitale*, A.M.N.H. No. 93447, from Barra do Tapirape, Mato Grosso, Brazil; and *L. octostegum*, M.H.N.P. No. 7055, from Brazil. Bottom row, left to right: *L. polystegum*, B.M. No. 1903.6.29.31, from Brazil, no locality (the arrow points to the precloacal pores); *L. scutigerum*, K.M. No. R4491, from Brazil, no locality; and *L. wuchereri*, N.M.W. No. 12373, from Porto Seguro, Bahia, Brazil.

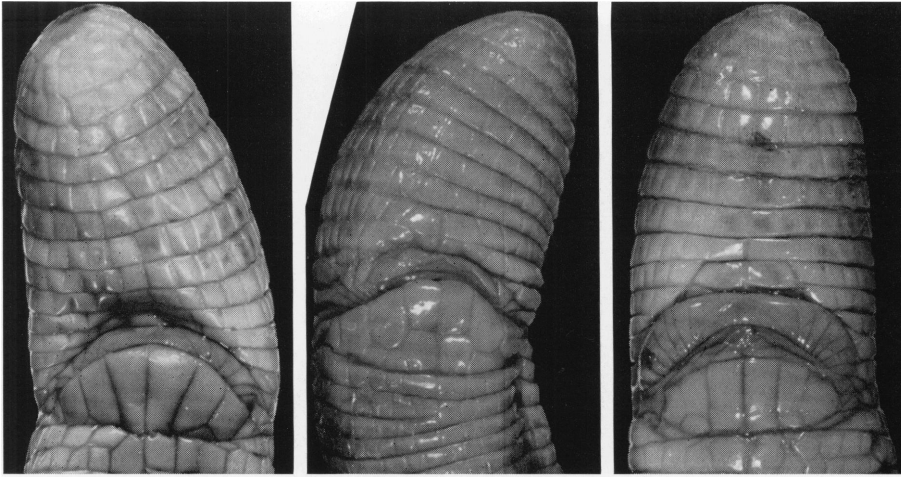


FIG. 49. *Leposternon microcephalum*. Ventral views of cloaca and tail. Left: N.M.W. No. 12369:6, from Joinville, Santa Catarina, Brazil. Middle: I.M.Z.U.T. No. 970, from Asuncion del Paraguay, Paraguay. Right: Z.S.M. No. 230/33A, from Serrinha, Sao Paulo, Brazil.

The fifth and also slender species, *L. scutigerum*, is clearly the most distinct in the genus by virtue of the fusion of the majority of its head shields into two enlarged, heavily keratinized plates. It is thus the only species of the genus with a heavy layer of keratin extending over the top of the head rather than, as in *L. polystegum*, covering only the rostronasal. The range of this species extends from Rio de Janeiro into Minas Gerais. Unfortunately, the range is so ill-defined as to leave it unclear whether it overlaps that of any species of *Amphisbaena*.

The last species is *L. infraorbitale*, a stouter and much larger form, whose poorly documented range may overlap that of *L. microcephalum*, *L. wuchereri*, and *L. scutigerum*, and possibly that of

either *L. octostegum* or *L. polystegum*. This, and a closely similar species appears to extend beyond the range of *L. microcephalum* in Mato Grosso.

Although it is not at all clear what permits the several kinds of sympatry among the species of *Leposternon* thus far discussed, it has already been suggested that *L. infraorbitale* occupies a zone suitable for a species of significantly larger body size and greater diameter. In contrast *L. scutigerum*, *L. polystegum*, *L. octostegum*, and *L. wuchereri* are more slender forms. Body size appears to be one of the factors permitting subdivision of the environment among the species of *Leposternon*, in a fashion similar to that already noted for the South American species of *Amphisbaena* (Gans, 1966).

KEY TO THE SPECIES

1. Only two rows of enlarged scales visible in dorsal view atop the head (the first of these the rostronasal, the second the azygous, which may be followed by a fringe of much smaller segments in the occipital region); suture pattern simple; pectoral region covered with large geometrically regular shields 2
- Three or more rows of enlarged shields atop the head, suture pattern often complex; pectoral region complex or not 3
2. Rostronasal followed by an enormous azygous shield which covers nearly the entire dorsal sur-

- face of the head, narrowly fringed posteriorly by a single row of very much smaller segments; head shield strongly keratinized; mental and postmental discrete; 253-305 postpectoral annuli *L. scutigerum*
- Rostronasal followed by a very large azygous, flanked on each side by triangular prefrontals and small temporals; head shields not significantly keratinized; a single mental-postmental segment; 378 postpectoral annuli *L. octostegum*
3. A single, very small first supralabial followed by a large second and a small third supralabial 4

Snout Vent length – mm

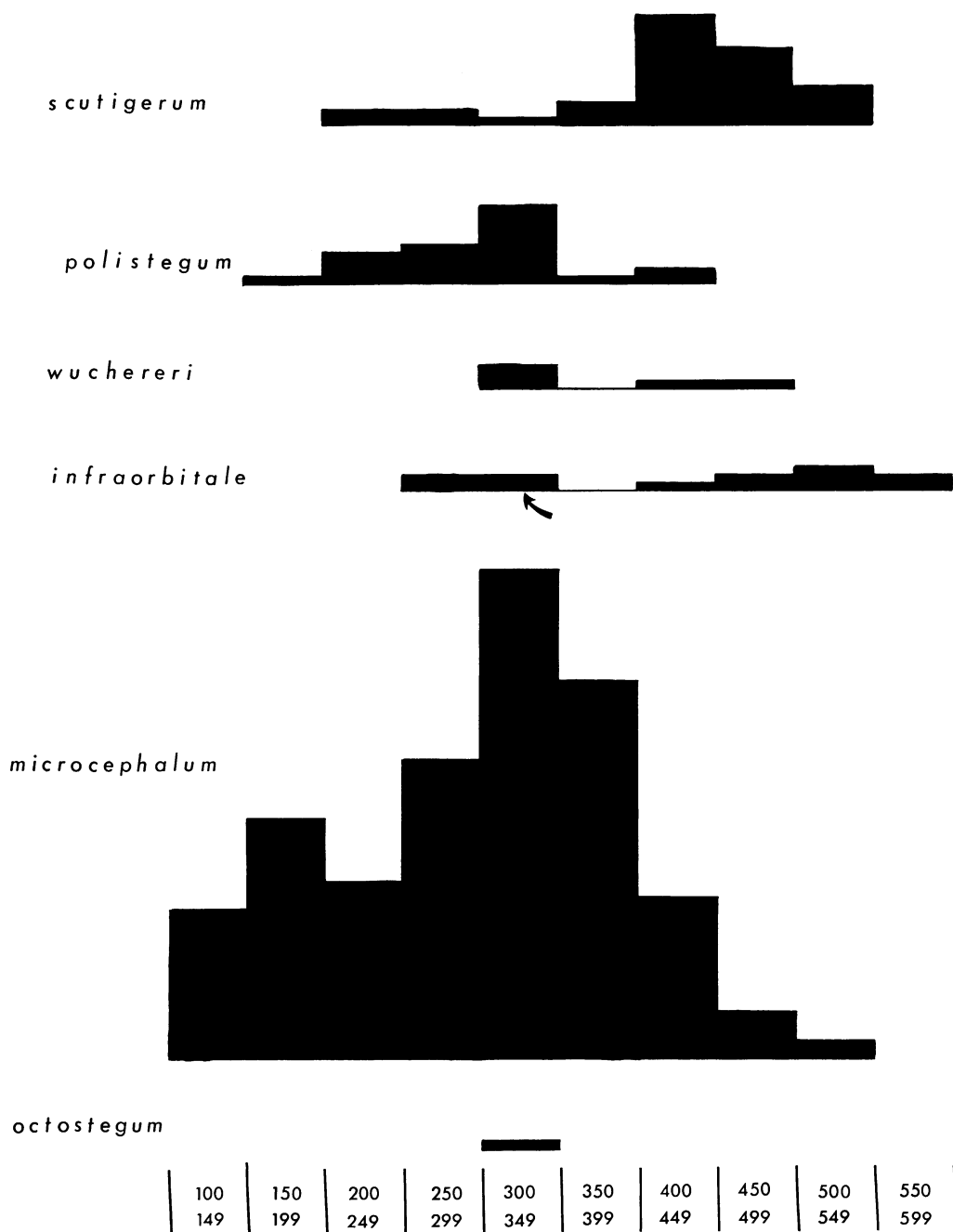


FIG. 50. *Leposternon*. Histogram for snout-vent length of several species of the genus. Vertical unit shown under *L. octostegum* represents a single specimen. The vertical scale in histogram for *microcephalum* has been halved to facilitate comparison. Arrow points to position of the specimen listed as *incertae sedis* with *L. infraorbitale*.

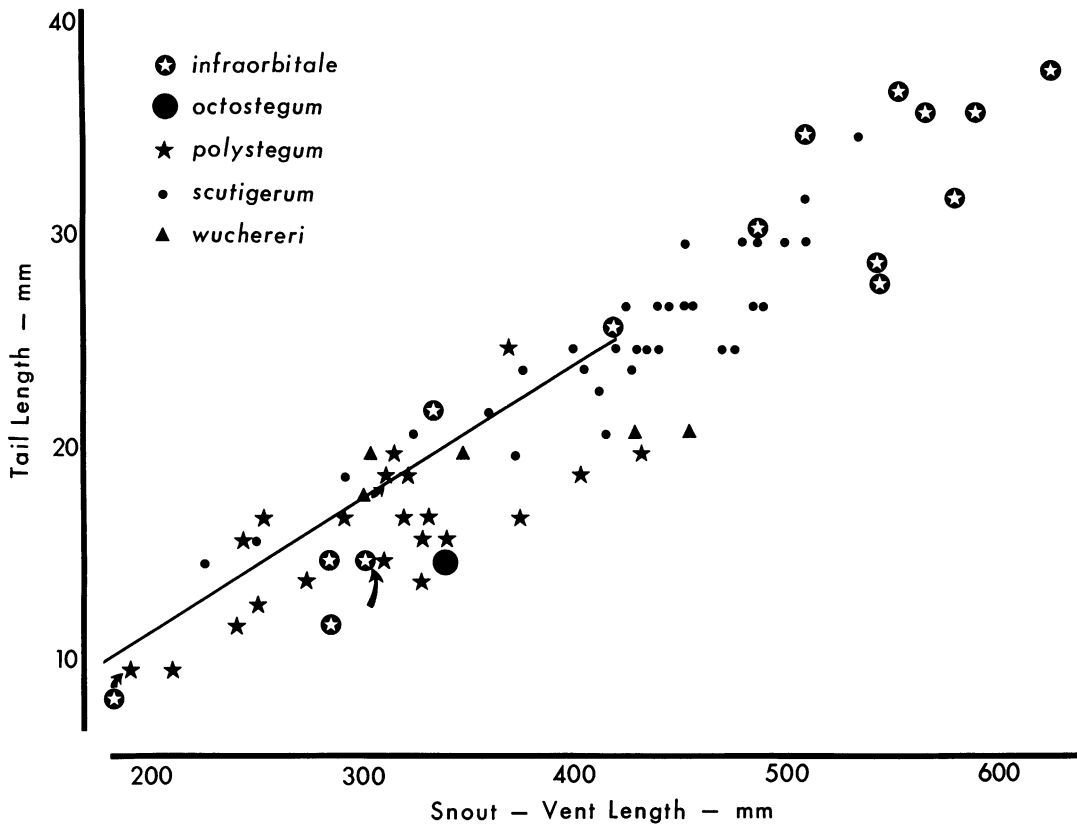


FIG. 51. *Leposternon*. Scatter diagram showing tail length versus snout-to-vent length for species *scutigera*, *polystegum*, *wuchereri*, *infraorbitale*, and *octostegum*. A regression line for sample of *L. microcephalum* from Santa Catarina is included for comparison. Compare with figure 43.

- A very large first supralabial followed by a smaller second supralabial 5
4. Azygous shield in contact with rostronasal; frontals and medial temporals much larger than the azygous, longer than wide and arranged in a characteristic linear grouping; infraocular absent; a small first followed by a large second intralabial; pectoral shields in a regular arrangement of large shields similar to an hourglass; dorsal number of postpectoral annuli generally equal to ventral, rarely up to 10 greater than; adults of medium size; (snout-vent length equals 205–432 mm.); one or two precloacal pores on each side of the precloacal shield *L. polystegum*
Azygous shield separated from contact with the rostronasal by a wide suture between prefrontals; frontals about as wide as long, not significantly larger than the azygous, temporals much smaller; generally an infraocular; a very large first infralabial; pectoral segments only slightly enlarged, rounded sometimes with irregular longitudinal fusions; precloacal pores lacking. . . 6
 5. Azygous invariably distinctly delineated; pectoral region covered by three to four pairs of elongate regularly arranged shields which may fuse except for the midline; number of dorsal and ventral postpectoral annuli more or less equal; 242 to 265 postpectoral annuli *L. wuchereri*
Azygous often fused in various ways with adjacent head shields; a medial pair of elongate pectoral shields, with other modified, possibly enlarged shields radiating out from these anteriorly; always significantly (5–25) more dorsal than ventral postpectoral annuli with the increase greater in the second-fifth, third-fifth, and fourth-fifth of the trunk; (177–242 postpectoral annuli) *L. microcephalum*
 6. Dorsal number of postpectoral annuli always five to 25 higher than ventral number; 95 to 100 body vertebrae; 236 to 275 ventral, and 259 to 304 dorsal, postpectoral annuli; 25.6 to 33 ventral and 22.3 to 31.4 dorsal segments per mid-body annulus; 10 to 13 caudal annuli; adults very large (snout-vent length equals 285–600

mm.) *L. infraorbitale*
 Dorsal number of postpectoral annuli 47 higher
 than ventral; 109 body vertebrae; 314 ventral,
 and 36 dorsal, postpectoral annuli; 42 ventral,

and 38 dorsal, segments per midbody annulus;
 16 caudal annuli; no information on adult size
 *L. species*

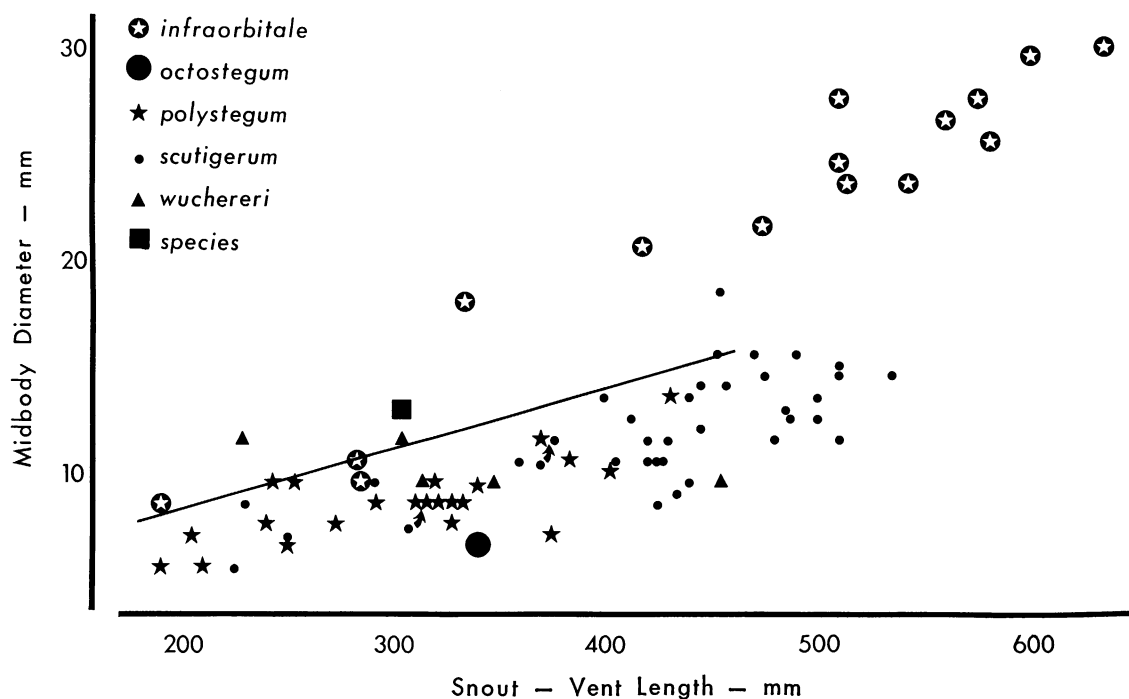


FIG. 52. *Leposternon*. Scatter diagram showing midbody diameter versus snout-to-vent length for the species *scutigerum*, *polystegum*, *wuchereri*, *infraorbitale*, and *octostegum*. A regression line for sample of *L. microcephalum* from Santa Catarina is included for comparison. Compare with figure 44.

TAXONOMIC SECTION

GENUS *LEPOSTERNON* WAGLER

Leposternon WAGLER, 1824, p. 70. Type species: *Leposternon microcephalus*, by monotypy.

Leposternon GRAY, 1825, p. 204 (emendation).

Lepidosternon WAGLER, 1830, p. 197 (emendation).

Cephalopeltis J. MÜLLER, 1832, p. 256. Type species: *Cephalopeltis cuvierii* (= *L. scutigerum* Hemprich), by monotypy.

Leposternum AGASSIZ, 1848, p. 205 (emendation).

Sphenocephalus GRAY, 1865, p. 452. Type species: *Leposternon grayii* = *L. polystegum*, by monotypy (junior homonym of: *Sphenocephalus* AGASSIZ, 1839, pp. 4, 129 [teleosts], *Sphenocephalus* FITZINGER, 1843, p. 25 [snakes], and *Sphenocephalus* BLYTH, 1853, p. 654 [lizards]).

ATTRIBUTION OF NAMES

Leposternon microcephalus was described by Wagler (1824) from the Spix Collection with the locality "dans les environs du village Mandioca, . . . près de la montagne dos Orgãos, sur un grand chemin bordé d'arbres, d'après une pluie tombée," in Rio de Janeiro, Brazil. As noted by Hellmich (1960) the holotype is Z.S.M. No. 3150/0; it was included in the analysis. The name, which was emended to *L. microcephalum* by Fitzinger (1826), clearly pertains to the most widely ranging species.

In 1825 Wied described *Amphisbaena punctata* from "Rio de Janeiro und am Flusse Espirito Santo, also in dem ganzen südlichen Brasilien." The American Museum of Natural History, which owns much of the Maximilian Collection, has a specimen (A.M.N.H. No. 1101) from "Rio de Janeiro, Brazil" bearing the indication "Maximilian."¹ The specimen which was available for analysis was in poor condition but the remaining characteristics were in good agreement with Wied's description. There can thus be little doubt that it represents the holotype, that the type locality is Rio de Janeiro, that this specimen pertains to the most widely ranging species, and that the name *punctata* is a strict synonym of *microcephalum*.

In 1829 F. G. Hemprich described a single specimen obtained by Olfers from "Brasilia" as

Amphisbaena scutigera. The paper was apparently presented at a meeting during 1817, but the volume containing it did not appear until 1829. The Berlin Museum contains a specimen (Z.M.U. No. 1398) listed as the holotype. There are some minor differences between it and the description (particularly in counts of body annuli), but the specimen which was available for the present study is presumably the holotype. Both specimen and description characterize, primarily by the heavily keratinized cephalic shields, the medium-sized species from Rio de Janeiro and Minas Gerais. The name *scutigerum*, as emended by Duméril and Bibron (1839, p. 509), is hence applicable to this species. Wilhelm Hemprich, who apparently attended the 1817 session, in 1820 used the name *Amphisbaena scutigerum* or "schildtragende Ringelschlange" in a popular natural history. As no description was then given the mention created a *nomen nudum* and the name *scutigerum* dates from 1829.

In 1831 Wiegmann and Ruthe (p. 186) erected the new name *Lepidosternon hemprichii* as a substitute for *Amphisbaena scutigera*.

In 1832 Johannes Müller published an extensive anatomical memoir in the course of which he described *Cephalopeltis cuvieri* based on a specimen from "Rio de Janeiro" in the Paris Museum. The description and illustration of the specimen mention enlarged keratinized head shields and the characteristic pectoral pattern and leave little doubt that the name *cuvieri* is a strict synonym of *scutigerum*. Duméril and Bibron (1839, p. 511), who listed the latter name with the designation "Nobis," although they referred to the papers of Hemprich and Müller, indicated that the two specimens then in the collection had been collected in "Brésil" by M. Galot, and the remaining one of these (M.H.N.P. No. 3125) is here designated as lectotype.

In 1834 Wiegmann erected the name *Lepidosternon maximiliani* as a substitute for *Amphisbaena punctata* Wied which he incorrectly believed to be preoccupied. The name is thus a strict synonym of *L. microcephalum*. In the same paper, the author again recognized *C. hemprichii* of Wiegmann and Ruthe and contrasted it to *C. cuvieri* Müller which he had never seen.

¹I earlier noted (Gans, 1967) that the holotype appeared lost but George Foley of the American Museum's Department of Herpetology, kindly pointed out my error.

In 1836 Wiegmann discussed the issue in detail. It becomes clear from description and illustrations that he recognized four species, *hemprichii*, *cuvieri*, *microcephalum* and *maximiliani*. Retention of *hemprichii* is based entirely on the absence in the type of the series of enlarged segments found in the occipital region of *cuvieri*. As this feature is occasionally found within this species, the names are strict synonyms. In the same paper (1836) Wiegmann also used the name *L. maximiliani* for a species considered different from *L. microcephalum* and based upon a specimen in the Berlin Museum. The specimen in question (apparently Z.M.U. No. 1395) shows the characteristic fusion of frontal and parietals occasionally seen in specimens from the vicinity of Rio de Janeiro. It differs in this from the type of *L. microcephalum* in which these segments are discrete. Wiegmann's illustration also shows the strong folding of the facial surface characteristic of specimens from Rio de Janeiro and slightly more southern regions. His discussion makes clear his opinion that species in the generic complex mentioned should be defined primarily on the basis of differences in head scalation. The name *L. maximiliani* whether dating to 1834 or 1836 then remains a strict synonym of *L. microcephalum*.

In 1839 Duméril and Bibron described *Lepidosternon phocaena* from a specimen collected in "Buenos-Ayres" by d'Orbigny. The holotype still remains in the Paris Natural History Museum (M.H.N.P. No. 488), but its assignment poses considerable problems. The individual represents the only specimen of the genus attributed to the Province of Buenos Aires, Argentina.¹ The museum there has an otherwise excellent collection of amphisbaenians but lacks any records of *Leposternon* for the region. The character pattern of the specimen does not resemble that of specimens from more northern regions of eastern Argentina, instead it is characteristic of material from Bolivia, and from the Province of Salta, Argentina.

The resemblance centers on a relatively small, shield-shaped azygous, surrounded by fairly large prefrontals, supraoculars, and frontals (see figs. 7-11, of pl. 6 in d'Orbigny, 1847). The pectoral pattern is characterized by an arrangement of unfused, relatively large, angular seg-

ments. A few isolated segments immediately ventral to the lateral line still show central pigment dots even though the specimen is soft and partially decomposed so that the bones show through the skin at midbody. The counts of anterior lateral annuli (14), postpectoral annuli (185)² and number of body vertebrae (87) fall within the range for Bolivian but not for eastern specimens. D'Orbigny (1847, p. 9) does indicate that this species occurs "principalement" in the province of Corrientes, Argentina, but he also collected in Bolivia and the type seems to have been collected there. Consequently the type locality is here corrected to read "Bolivia." Under the circumstances the name appears available for the western race of *Leposternon microcephalum*.

In 1848 A. Smith used the combination "*Lepidosternon macrocephalum*, Wag." This is an obvious *lapsus* and hence not available under the code (Stoll and others, 1961).

In 1851 A. Duméril described two new species, *Lepidosternon Polystegum* and *L. Octostegum*, based upon single specimens then in the Paris Museum, and collected respectively in "Bahia" by M. Lemelle-Deville (M.H.N.P. No. 3134), and "Brésil" (M.H.N.P. No. 7055). The latter form was figured by Peters (1879, fig. 1). The descriptions emphasized the number and arrangement of cephalic shields, the arrangement of pectoral shields, and the number of caudal annuli. The descriptions include annular counts for *L. polystegum* but not for *L. octostegum* and are in good agreement with the types which were available for this analysis. It is clear that both names pertain to valid species, the former to the assemblage with narrowed frontals from the northeast of Brazil, and the latter to the unique individual considered distinct because of the remarkably high number of body annuli, and other characteristics cited by Duméril.

In 1859 Berthold provided a brief diagnosis of *L. infraorbitale* based upon a specimen from "Bahia" then in the zoological museum at Göttingen. The diagnosis noted the presence of an infraocular, three supralabials, subdivided pectorals, 15 anterior laterals, and 269 body (=postpectoral) annuli. An unnumbered specimen in the Göttingen collection (G.U.M.), labeled type, was available for this analysis, and

¹The specimen of that locality referred to by Gray (1865) was not determinable.

²Strauch (1881, col. 96) noted that the count given in the original description is too high as it includes some 15 intercalated dorsal half-annuli.

perfectly fits the original description (as well as the detailed version furnished by Strauch, 1881, col. 98). The name *L. infraorbitale* is then available for the large species of *Leposternon* characterized by the presence of infraoculars and small first supralabials.

In 1865 Gray published the manuscript name *L. Grayii* A. Smith based on a specimen from "South America." The holotype (B.M. No. 48.6.26.11:RR1946.9.1.7) was available for analysis during a visit to the British Museum. Gray's description figured dorsal and ventral views of the anterior end of the type. His description mainly emphasized geometrical details of the cephalic and pectoral segmentation. Segments of the chin region of the type show some irregularity, but other counts and character states indicate that this is a specimen of *L. poly-stegum* and the name *L. grayii* hence belongs in the synonymy of that species. As part of the description Gray erected the subgeneric name *Sphenocephalus* for this species; however, this name is three times a junior homonym having been used by Agassiz (1839) for a fish, by Wiegmann (1843) for a snake and by Blyth (1853) for a lizard.

In 1879 Peters in a brief paper reviewed the South American forms with dorsoventrally compressed heads and described the new species *Lepidosternon wuchereri* based upon a single specimen (Z.M.U. No. 9389) obtained with the collection of a Dr. Wucherer of Bahia. Thus the type locality, normally listed as "Bahia," is in doubt. The specimen that was available for analysis is in good agreement with the description and confirms the fact that the name pertains to the species from north of Rio de Janeiro and is distinguishable by a large azygous shield, medium to high numbers of postpectoral annuli, and an arrangement of multiple, more or less parallel pectoral shields.

In 1881 Strauch published the result of a very extensive study based upon a reexamination of most materials then in European museums, and particularly on the rich collection amassed in St. Petersburg (now Z.I.L.). During analysis, he apparently prepared the counts of all specimens. The plates to the work, although prepared in part (Gans, In press), were never published. Strauch's (1881) account marks a milestone in our understanding of the Amphisbaenia. Most of the forms recognized or described by him proved to have been valid. Yet he

described four new South American species of *Lepidosternon*, all of which belong in synonymy. This observation as much as anything else emphasizes the drastically different magnitude of character variation in this segment of the order.

The first name was *Lepidosternon rostratum* based upon two poorly preserved specimens (Z.I.L. Nos. 314 and 315), the first of which is here designated as lectotype because of Strauch's statement that it formed the basis for the description. The specimens from "Bahia" (provided in 1837 by Luschath) were available for this analysis. Strauch emphasized that *L. rostratum* differed from *L. infraorbitale* in the absence of infraoculars, a character that shows some variation in the series assembled for the latter form. The types do not lack infraoculars but show a ventrad displacement of the raphe crossing the third supralabial. The infraocular is thus very large and lies in point contact with the labial edge, whereas the supralabial proper is restricted to a small triangular area. As all other differences noted by Strauch were found to vary within the available series, the name *L. rostratum* becomes a strict synonym of *L. infraorbitale*.

The second new name proposed by Strauch was *L. Petersi* based upon a specimen from "Brasilien" (Z.M.U. No. 1396) in the Berlin Museum, which was available for this analysis. Counts and most other characteristics noted by Strauch are in reasonable agreement with the holotype, except for the supposed presence of small first infralabials considered diagnostic by Strauch. These are absent. The specimen does show a fold partially separating off the anterior tip of the large left infralabial, but this is clearly an artifact of preservation. Strauch noted that he discovered this form to be distinct after it had been returned to the Berlin Museum and described some characteristics from the drawings. It thus seems likely that the artist provided the original error. As all other characteristics of the specimen agree with those described for *L. microcephalum* from coastal Brazil the name *L. petersi* belongs in the synonymy of that form.

The third name is *Lepidosternon crassum* based upon Z.I.L. No. 316 from "Brasilien" collected by Dr. Tonget (1867). In diagnosis Strauch stressed the aberrant segmentation of the dorsal surface of the head, as well as the relatively elongate head and stout body. Yet the latter two proportions are extremely difficult to measure

accurately in curved specimens. The measurement obtained by me suggests that the body diameter is actually of the same order as measurements of specimens of *L. microcephalum*, and thus invalidates this characteristic. The pattern of the head shields, particularly the fusion of the azygous, frontals, and supraoculars, is characteristic for specimens of *L. microcephalum* from the vicinity of Rio de Janeiro. All other characteristics suggest that the holotype is a very large specimen of that species and that the name *L. crassum* is a strict synonym.

The fourth name was *L. Guentheri*, based upon a specimen "angeblich von Brasilien." The holotype (Z.I.L. No. 313) was examined. Strauch emphasized the aberrant segmentation of the occipital and pectoral regions. Both of these and the other characteristics of the individual are well within the range of variation seen in specimens of *L. microcephalum*. The cephalic segmentation is distinguished by the wide contact between azygous and rostronasal, flanked by two straight-sided and clearly separated prefrontals. This pattern is seen to characterize specimens from inland Sao Paulo as well as those from north-central Argentina and adjacent Paraguay (fig. 20). The chin of the holotype shows the postmental flanked and kept from contact with the infralabials by an elongate pair of malars, an arrangement characteristic of specimens from northeastern to central Argentina (fig. 21). The fusion of the central rows of segments in the pectoral region occurs most commonly in Brazil (fig. 22). The combination of characters suggests that the type was presumably collected near the Rio Grande do Sul-Corrientes frontier, but the scarcity of records for that region makes the prediction uncertain. The name is then a synonym of *L. microcephalum*.

In 1885 Boettger presented a report on the collection made by H. Rohde in Paraguay. Boettger named each of the four specimens of *Leposternon* as the holotype of a new species. The Rohde collection was the property of an Institut Linnaea then in Frankfurt am Main, Germany. Investigation discloses that this was a commercial group and that the holotypes and some other material described by Boettger were bought by Strauch (cf. Gans, 1966, p. 232). All are now in the Leningrad collection and were examined for the present analysis.

The four new species described by Boettger (1885) are all based upon variants of *L. micro-*

cephalum from Paraguay. *Lepidosternon Boulengeri* (Z.I.L. No. 6656) is based on a specimen with narrow contact between azygous and rostronasal, fusion of supraoculars and prefrontals, and very elongate malars intercalating between the infralabials and postmentals. The pectoral region shows no fusion of segments.

The type of *Lepidosternon Strauchi* (Z.I.L. No. 6655) shows a small shield-shaped azygous, enormous prefrontals fused with supraoculars and much smaller pairs of malars, as well as a chin segmentation characterized by much smaller pairs of anterior malars that lie along the middle to posterior portion and flank the posterior portions of the postmental.

The holotype of *Lepidosternon affine* (Z.I.L. No. 6654) shows the azygous shield-shaped, in point contact with the rostronasal, and flanked by well-defined preoculars and oculars. The first and second infralabials are fused and there are two pairs of malars and no pairs of postgenials.

The holotype of *L. onychocephalum* (Z.I.L. No. 6653) is similar to that of *L. boulengeri* except that the contact between azygous and rostronasal is much wider (fig. 6B) and the second supralabial relatively large. The last two forms also have the higher numbers of counts of postpectoral annuli characterizing certain Paraguayan individuals. The chin region shows no fusion.

In 1885 Boulenger named and illustrated (1885b, p. 466, pl. 24, fig. 5) *Lepidosternon boettgeri* based upon a single specimen (B.M. No. 81.11.5.1:RR1946.8.8.59) from "Corrientes, Argentina." Boulenger's key emphasized the proportions of the head shields whose arrangement is similar to that of the type of *L. boulengeri*, although asymmetrical. The ventral surface of the head shows single, enlarged infralabials, and several malars arranged in two rows but not separating the postmental from contact with the first infralabials. The segments of the pectoral region show no fusion. The name hence belongs in the synonymy of *L. microcephalum*.

In 1894 Boulenger (1894a) described the new species *L. latifrontale* based upon a series of nine specimens obtained from Dr. J. Bons "near Asuncion, Paraguay" and examined in the British Museum. Of these, B.M. No. 94.314.31:RR1946.8.8.91 is here chosen as lectotype because it matches the dimensions given by Boulenger. Unfortunately, however, its vertebral column is broken and this appears to have been

true when Boulenger examined it. The general pattern of cephalic segmentation is that shown in figure 6C, but the variation is extreme and no two specimens match perfectly. The variability of the dorsal surface involves a more or less clear definition of the supraocular, the separation or fusion of parietals and occipitals, and the length of the distance to which the sutures dividing the supraoculars-prefrontals from the azygous extend. Many specimens have asymmetrical arrangements.

On the ventral surface there is an extensive and irregular fusion of the first and second infraorbitals and malars. The segments of the pectoral region show some slight enlargement but are insignificantly subdivided. Under the circumstances, it appears as though Boulenger was describing a local variant of *L. microcephalum* so that the name *L. latifrontale* belongs in the synonymy of this species.

In 1895 Peracca (1895a) described two new species from a collection made by Alfredo Borelli in Argentina and Paraguay. The first of these is *L. Borellii*, the holotype of which (I.M.Z.U.T. No. 971) came from "Chaco argentino (Resistencia)" and refers to a specimen with a head pattern (configuration C, fig. 20) showing discrete supraoculars and an azygous that does not contact the rostronasal, coupled with characteristically high numbers of body annuli. The second form, *L. Camerani*, whose type (I.M.Z.U.T. No. 972) came from "Luque (Paraguay)" shows the *L. guentheri* conformation on the dorsal surface of the head, with the azygous in medium contact with the rostronasal; it thus marks the third time that this pattern has been named. Peracca's decisions that he was dealing with distinct species were also based upon the geometry of the parietal-occipital region and the names must thus be included in the synonymy of *L. microcephalum*.

In the same year Peracca (1895b) described *Lepidosternon sinuosum* from "Brasile" based on a specimen from the Turin Museum (I.M.Z.U.T. No. 1108) and used in this analysis. He compared the new form with *L. wuchereri* of Peters but was very impressed with the sinuous form of the cephalic sutures and the (relatively slight) differences in number of body annuli. The type, which was available for examination, clearly belongs to Peters's species and the name *L. sinuosum* in its synonymy.

In 1904 Peracca described two additional

species. *Leposternon laticeps* was based on three specimens (I.M.Z.U.T. No. 2749) collected at "Urucum, Mato Grosso, Brazil" and available for this analysis. Except for the low values of ventrally (but not dorsally) counted postpectoral annuli, these specimens show the typical character pattern of the Bolivian variant of *L. microcephalum*, and the name belongs in the synonymy of that species.

The second new name was *L. carcani* based upon a single specimen (I.M.Z.U.T. No. 2750) from "Tebicuari, Paraguay." This is an individual with the shield-shaped azygous not in contact with the rostronasal and with oculars and prefrontals fused. All characteristics of the individual show good agreement with those of one of the Paraguayan variants of *L. microcephalum* and this name also belongs in the synonymy of that species.

In 1910 Werner erected the name *Lepidosternon pfefferi* for a specimen from Paraguay in the Hamburg Museum. The holotype was destroyed during World War II. The diagnosis noted that this form was most closely related to *L. boettgeri* from which it is supposed to differ by a more obtuse snout tip, parietals that are wider than long, an eye not clearly visible through the head shields, and a temporal smaller than the supraoculars. The description noted that the number of body annuli was $281 + 17$, that snout-vent plus tail length was $385 + 20$ mm. and that the dorsal surface was brownish, whereas the ventral surface was a dirty white. None of the differences adduced appears to represent more than individual variation and this, the eighth specific name erected on the basis of a Paraguayan specimen, also belongs in the synonymy of *L. microcephalum*.

In 1936 K. P. Schmidt described *Leposternon polystegoides* based upon five specimens from Lake Papari (now Nisia Floresta), Rio Grande do Norte then in the California Academy of Sciences. Three of these (C.A.S. No. 49866, F.M.N.H. Nos. 64425 and 64426) were available for the present analysis. Schmidt correctly noted that the body counts were unusually low and that the azygous (his frontal) invariably was in contact with the rostronasal. Yet neither characteristic supports the concept that this form is sampled from a distinct species, particularly in view of the several hundred miles separating the records of this form from the next ones of typical *L. polystegum*. Both head pattern and vertebral

numbers of the types are furthermore in good agreement with those of specimens from adjacent Pernambuco even though their counts of dermal annuli differ so drastically. Under the circumstances, it seems most appropriate to place this

name into the synonymy of *Leposternon poly-stegum* with the understanding that it remain available for a northeastern race should further study confirm the existence of one.

ACCOUNTS OF THE SPECIES

Leposternon infraorbitale (Berthold)

Lepidosternon infraorbitale BERTHOLD, 1859, p. 179. *Terra typica*: "Bahia," Brazil. Holotype: G.U.M. (no number).

Lepidosternon rostratum STRAUCH, 1881, col. 99. *Terra typica*: "Bahia." Lectotype: Z.I.L. No. 314 (by present designation). Lectoparatype: Z.I.L. No. 315.

DISTRIBUTION RECORDS: BRAZIL:—S.M.F. Nos. 11847, 11848 (Boettger, 1893). *Mato Grosso*:—Barra do Tapirape: A.M.N.H. Nos. 93447, 93448. Chapada (Chapada, 30 miles northeast of Cuyabá and near the headwaters of the Xingu, a tributary of the Amazon): A.N.S.P. No. 13004 (Cope, 1887). *Pernambuco*:—M.G. No. 1010.77. *Bahia*:—B.M. No. 88.11.5.1 (Boulenger, 1890); G.U.M. (unnumbered) (holotype *L. infraorbitale*; Berthold, 1859; Strauch, 1881); Z.I.L. Nos. 314 (lectotype *L. rostratum*; Strauch, 1881), 315 (lectoparatype *L. rostratum*; Strauch, 1881). *Espirito Santo*: Santa Teresa: M.N. Nos. 1775C, 1775D. Vitoria, on Paraizo do Sul: Z.S.M. No. 457/1920. *Minas Gerais*: Fazenda Paraopeba (?near Rio Paraopeba, on right bank of Rio São Francisco): M.N. No. 1782. *Rio de Janeiro*:—M.C.Z. No. 1363.

BIOLOGY: The hemipenes of this species were described by Rosenberg (1967).

Leposternon microcephalum Wagler

Leposternon microcephalum WAGLER, 1824, p. 70. *Terra typica*: "Dans les environs du village Mandiocca, . . . près de la montagne dos Orgãos, sur un grand chemin bordé d'arbres," Rio de Janeiro, Brazil. Holotype: Z.S.M. No. 3150/0.

Amphisbaena punctata WIED, 1825, p. 500. *Terra typica*: "Bei Rio de Janeiro und am Flusse Espirito Santo," Brazil. Holotype: A.M.N.H. No. 1101 (senior homonym of *A. punctata* Bell [= *Cadea blanoidea*]).

Leposternon microcephalum FITZINGER, 1826, p. 53 (justifiable emendation).

Lepidosternon maximiliani WIEGMANN, 1834, p. 21. (New name for *A. punctata* Wied. Redescribed in Wiegmann, 1836, p. 154, where it was considered a distinct species based on Z.M.U. No. 1395 from "Brazil.")

Lepidosternon macrocephalum A. SMITH, 1848 (1834–1849), pl. 67 (*lapsus* for *L. microcephalum*, not available; Stoll and others, 1961, art. 33b).

Lepidosternon phocaena DUMÉRIL AND BIBRON, 1839, p. 507. *Terra typica*: "Buénos-Ayres," Argentina, here corrected to "Bolivia." Holotype: M.H.N.P. No. 488.

Lepidosternon petersi STRAUCH, 1881, col. 103. *Terra typica*: "Brasilien" (probably vicinity of Rio de Janeiro). Holotype: Z.M.U. No. 1396.

Lepidosternon crassum STRAUCH, 1881, col. 106. *Terra typica*: "Brasilien" (probably vicinity of Rio de Janeiro). Holotype: Z.I.L. No. 316.

Lepidosternon güntneri STRAUCH, 1881, col. 110. *Terra typica*: "Unbekannt, wahrscheinlich Brasilien" (probably north-central Argentina). Holotype: Z.I.L. No. 313.

Lepidosternum boulengeri BOETTGER, 1885, p. 220. *Terra typica*: "Paraguay, Amer. merid." Holotype: Naturhistorisches Institut Linnea, Frankfurt-am-Main, now Z.I.L. No. 6656.

Lepidosternum strauchi BOETTGER, 1885, p. 221. *Terra typica*: "Paraguay, Amer. merid." Holotype: Naturhistorisches Institut Linnea, Frankfurt-am-Main, now Z.I.L. No. 6655.

Lepidosternum affine BOETTGER, 1885, p. 223. *Terra typica*: "Paraguay, Amer. merid." Holotype: Naturhistorisches Institut Linnea, Frankfurt-am-Main, now Z.I.L. No. 6654.

Lepidosternum onychocephalum BOETTGER, 1885, p. 224. *Terra typica*: "Paraguay, Amer. merid." Holotype: Naturhistorisches Institut Linnea, Frankfurt-am-Main, now Z.I.L. No. 6653.

Lepidosternon boettgeri BOULENGER, 1885b, p. 466. *Terra typica*: "Corrientes, Argentina." Holotype: B.M. No. 81.11.5.1: RR1946.8.8.59.

Lepidosternum latifrontale BOULENGER, 1894a, p. 345. *Terra typica*: "Near Asuncion, Paraguay." Lectotype by present designation: B.M. No. 94.314.31: RR1946.8.8.91. Lectoparatypes: B.M. Nos. 94.314.27: RR1946.8.8.87–94.314.30: RR1946.8.8.90; 94.314.32: RR1946.8.8.92–94.314.35: RR1946.8.8.95.

Lepidosternum borellii PERACCA, 1895a, p. 10. *Terra typica*: "Chaco argentino (Resistencia)." Holotype: I.M.Z.U.T. No. 971.

Lepidosternum camerani PERACCA, 1895a, p. 12. *Terra typica*: "Luque (Paraguay)." Holotype: I.M.Z.U.T. No. 972.

Lepidosternon laticeps PERACCA, 1904, p. 3. *Terra typica*: "Urucum," Mato Grosso, Brazil. Syntypes: I.M.Z.U.T. No. 2749 (three specimens).

Lepidosternon carcani PERACCA, 1904, p. 5. *Terra typica*: "Tebicuari," Paraguay. Holotype: I.M.Z.U.T. No. 2750.

Lepidosternon pfefferi WERNER, 1910, p. 35. *Terra typica*: "Paraguay." Holotype: Formerly in the Zoologischen Museum, Hamburg, destroyed.

DISTRIBUTION RECORDS: No Locality: A.Z.M. No. 10178; F.M.N.H. Nos. 9020, 9022–9025; K.M. Nos. R4475, R4476, R4480, R4485, R4487, R4489, R4490, R4493; N.M.B. No. 3822; N.M.W. Nos. 500.10, 500:1–500:13, 500:15–500:24; R.M.N.H. No. (unnumbered); S.M.F. Nos. 11824, 11844–11846; S.M.N.S. No. 443 (this is not the specimen

from "Bahia" identified as *L. wuchereri* by Strauch, 1881; counts and measurements differ markedly); Z.I.L. No. 2802; Z.M.U. No. 26332.

BRAZIL:—A.M.N.H. No. 27351 (Burt and Burt, 1931); A.N.S.P. Nos. 9669, 14359, 14360; B.U.M. Nos. 276, 771; H.M. Nos. 310, 502, 1202, 1972, 2202:1–2202:14; I.M.Z.U.T. No. 1180; K.M. Nos. R4478, R4481; M.C.Z. Nos. 2916, 3733; M.G. No. 1010.76; M.H.N.P. Nos. 484, 1665, 3122, 3123 (lectotype of *L. cuvieri*, Duméril and Bibron, 1839; Wiegmann, 1836), 5473, 5473A; M.L.U. Nos. 4, 5A, 5B, 7, 11–11B; N.H.M.G. No. 1122; N.M.B. No. 3823 (F. Müller, 1885A); N.M.W. Nos. 7, 13, 30, 8163:1–8163:4, 12363:5–12363:7; S.M.N.S. No. 4697; U.S.N.M. No. 58737 (Burt and Burt, 1930); Z.I.L. Nos. 313 (holotype *L. guentheri*, Strauch, 1881), 316 (holotype *L. crassum*, Strauch, 1881); Z.M.U. Nos. 1395 (holotype *L. maximiliani*, Wiegmann, 1836), 1396 (holotype *L. petersi*, Strauch, 1881), 11529, 26260; Z.S.M. No. 2623/0 (Gray, 1844). *Amazonas*:—M.N. No. 1776. *Mato Grosso*: Urucum: I.M.Z.U.T. Nos. 2749A–2749C (syntypes of *L. laticeps*, Peracca, 1904). *Pará*: N.H.M.B. Nos. 66D, 68A, 68B. *Pernambuco*:—B.M. No. 1903.12.3.8. *Bahia*:—(Strauch, 1881); M.C.Z. Nos. 1230, 98294–98296; N.M.W. Nos. 26A, 26B. Ilheos River (Strauch, 1881). São Bento dos Lagos: *Z.S.M. No. 280/1925. Andaraí: N.M.B. No. 3821 (F. Müller, 1885b); Z.M.U. No. 9388. *Espírito Santo*:—N.M.W. Nos. 27A, 27B (Strauch, 1881). Santa Teresa: M.N. Nos. 1775A, 1775B. Mimoso: B.M. No. 1914.3.20.2; S.M.F. No. 8284; Z.S.M. No. 42/1918 (L. Müller, 1927). Colonia Santa Leopoldina: S.M.F. No. 30260. *Minas Gerais*: Rio das Velhas, north of Bello Horizonte: B.M. No. 26.3.16.12. Morroqueim: K.M. No. R4477 (Reinhardt and Lütken, 1861). *Rio de Janeiro* (and *Guanabara*):—A.M.N.H. No. 1101 (holotype *A. punctata* Wied, 1825; *Lepidosternon maximiliani* Wiegmann, 1834; Burt and Burt, 1931); B.M. No. 74.5.21.8; C.G. Nos. 3087, 3720; H.M. No. 4398; K.M. No. R4479; M.C.Z. Nos. 1015, 98290–98293; N.M.W. Nos. 12363:1–12363:4; S.M.F. Nos. 21352, 30261 (L. Müller, 1927); S.M.N.S. Nos. 5018A–5018D; U.S.N.M. (unnumbered); Z.I.L. Nos. 5568–5570 (Gray, 1865, 1872, 1873; Strauch, 1881; Witte, 1930). *Pôrto Real*: B.M. Nos. 92.11.22.1–92.11.22.3; R.M.N.H. Nos. 5988A–5988O. Mendez: H.M. No. 2900; M.C.Z. Nos. 2902, 98297, 98298; S.M.F. No. 36221. Teresópolis: N.M.W. Nos. 12361:1–12361:7. Colonia Alpina, in vicinity of Teresópolis: N.H.M.B. Nos. 1, 2 (Goeldi, 1897). Nova Friburgo: Z.I.L. No. 3565 (Strauch, 1881). Cachoeiras: K.M. Nos. R4482–R4484, R4486, R4488. Petrópolis: H.M. No. 2200; M.N. Nos. 1778A, 1778F. Caxias: M.N. No. 1774. Barro Branco, near Caxias: M.N. Nos. 1767A, 1767B. Rio de Janeiro, Gb.: (Goeldi, 1897). Guanabara, Gb.: M.N. Nos. 3261, 3262, 3265. Quinta da Boa Vista, Gb.: M.N. Nos. 1773, 1783, 3267, 3269, 3270;

U.M.M.Z. Nos. 103077A, 103077B. Villa Isabel, Gb.: M.N. Nos. 3264, 3268. Covanca de Sarapui, Gb.: M.N. No. 1768. Represa dos Ciganos, Gb.: M.N. No. 3266. Santa Cruz, Gb.: N.M.W. No. 24. Serra dos Orgãos, Gb.: (Goeldi, 1897). Mandiocca, Serra dos Orgãos, Gb.: Z.S.M. No. 3150/0 (holotype *L. microcephalum* Wagler, 1824; Gray, 1825; Griffith and Pidgeon, 1831; Wiegmann, 1836; Hellmich, 1960). Tijuca, Gb.: S.U. No. 16102; U.M.M.Z. No. 103076. Bois de Sertão, Tijuca, Gb.: M.H.N.P. Nos. 02–371, 02–372. Angra dos Reis: M.N. No. 1762. Parati: M.N. Nos. 1755A, 1755B. *Sao Paulo*:—H.M. Nos. 1388A–1388C; I.M.Z.U.T. No. 1837; M.C.Z. Nos. 20659–20661, 27677; Z.S.M. Unnumbered. São Laureço: N.M.W. No. 18. Queimada Grande (Isl.): S.M.F. Nos. 57913–57918; (Mertens, 1955). Fazenda Ipanema, vicinity of: F.M.N.H. Nos. 69954, 69955. Ilha dos Buzios: S.M.F. Nos. 57911, 57912. Piquete: B.M. Nos. 1901.1.29.6, 1901.1.29.7. Serrinha: Z.S.M. Nos. 230/33A–230/33L (Hellmich, 1960). Santos: B.M. No. 94.6.29.27; H.M. Nos. 1660, 2870; (Ihering, 1898). *Paraná*:—S.M.F. Nos. 57685, 57686. *Santa Catarina*:—A.Z.M. No. 10176; G.U.M. No. 1913; N.H.M.G. No. 763; N.M.W. Nos. 25A–25E, 12362; Z.I.L. No. 7943. Rio Humboldt, Serra do Mar: U.S.N.M. Nos. 40221–40224 (Burt and Burt, 1930). Hansa: B.M. Nos. 1928.11.5.126–1928.11.5.129; S.M.F. Nos. 8248, 11823, 11835–11838, 30247–30250; Z.M.U. Nos. 31987A–31987C, 32010. Blumenau: B.M. No. 95.3.6.6. Humboldt (Itapecu River): H.M. Nos. 5286:1–5286:3, 3977:1–3977:16; M.N. Nos. 1780A–1780Z + 1780A'–1780S' (45 specimens), 1785A–1785C; S.M.N.S. Nos. 4849A–4849C. Joinville: H.M. Nos. 3570:1–3570:4, 3975A–3975D, 3976:1–3976:16; M.N. No. 1760; N.M.W. Nos. 33A–33E, 12364:1–12364:8, 12365:1–12365:5, 12366:1–12366:24, 12367:1–12367:3, 12368:1–12368:5, 12369:1–12369:11, 12370:1–12370:10, 12371:1–12371:24; S.M.F. Nos. 11841–11843. Teresópolis: B.M. Nos. 88.9.21.4–88.9.21.7; S.M.F. Nos. 11839, 11840. *Rio Grande do Sul*:—Z.I.L. No. 7608.

URUGUAY:—M.N.H.M. No. 903 (Devincenzi, 1925).

ARGENTINA:—H.M. No. 4329; M.A.C.N. Nos. 17887–17889, 17889; N.M.W. No. 16376; U.S.N.M. Nos. 73510–73512 (Burt and Burt, 1930; Lieberman, 1939); Z.M.U. No. 14035. *Salta*:—I.N.M. Nos. 50, 109; M.A.C.N. No. 17885, Rio Pescado: I.M.L. No. 00326. *Formosa*: "Reduccion," "Bartolomé de las Casas" (Department Palnio, latitude 25°24'S., longitude 59°35'W.); M.A.C.N. No. 5835. *Chaco*: Chaco Austral, on Rio Paraguay: H.M. No. 4793. Resistencia: I.M.Z.U.T. No. 971 (holotype *L. borellii*, Peracca, 1895a). Loma Plata, Menno Colony: K.U. No. 73448. Mouth of Rio de Oro: K.M. No. R4497. *Misiones*: San Ignacio: M.A.C.N. No. 4074. Cerro Santa Anna: (Masi, 1911). *Corrientes*:—B.M. No. 81.11.5.1:RR1946.8.8.59 (holotype *L. boettgeri*,

Boulenger, 1885b). Manantiales: M.A.C.N. Nos. 14695, 14696, 14949–14951. Apipe: M.A.C.N. No. 7973. *Entre Rios*: Concordia: M.N.H.M. No. 270. Concepcion del Uruguay: M.A.C.N. No. 3557. Nueva Escocia: M.A.C.N. No. 11984. Villa Urquiza: M.S.N.G. (Unnumbered). *Buenos Aires* (see Bolivia). *Rio Negro de Patagonia*:—M.G. No. 1010.75.

BOLIVIA:—Originally "Buénos-Ayres," here restricted to "Bolivia": M.H.N.P. No. 488 (holotype *Lepidosternon phocaena*, Duméril and Bibron, 1839; d'Orbigny, 1847, pl. 6, fig. 7–11); N.M.W. No. 12325. *Santa Cruz*:—U.M.M.Z. Nos. 63111, 68112A, 68112B, 68113. Sara: B.M. No. 1907.10.31.18; C.M. No. 1047 (Griffin, 1917). Rio Surutu (Bond and Schauensee, 1942, p. 317): U.M.M.Z. Nos. 63297, 63298, 63299A–63299C, 63300, 63301. Buenavista: B.M. Nos. 1927.8.1.165–1927.8.1.167; F.M.N.H. Nos. 35666, 35667; M.A.C.N. No. 3217; M.C.Z. No. 20624; R.M.N.H. Nos. 5242A, 5242B; U.M.M.Z. Nos. 60518, 60617A, 60617B, 60651, 60652.

PARAGUAY:—H.M. No. 3438 (Werner, 1910); M.A.C.N. No. 17886; N.H.M.B. No. 69A; N.M.B. Nos. 3816 (F. Müller, 1890), 3818–3820; N.M.W. Nos. 10, 12374, Z.I.L. Nos. 6653 (holotype *L. onychcephalum*, Boettger, 1885), 6654 (holotype *L. affine*, Boettger, 1885), 6655 (holotype *L. strauchi*, Boettger, 1885), 6656 (holotype *L. boulengeri*, Boettger, 1885). San Bernardino: Z.M.U. No. 26267. Tebicuari: I.M.Z.U.T. No. 2750 (holotype *L. carcani*, Peracca, 1904). Asuncion del Paraguay: H.M. No. 1654; I.M.Z.U.T. No. 970 (Peracca, 1895a); K.M. No. R443; S.M.F. Nos. 11849, 11850. Near Asuncion: B.M. Nos. 94.314.27:RR1946.8.8.87–94.314.30:RR1946.8.8.90 (lectoparatypes, *L. latifrontale*), 94.314.31:RR1946.8.8.91 (lectotype, *L. latifrontale*), 94.314.32:RR1946.8.8.92–94.314.35:RR1946.8.8.95; M.C.Z. No. 10783 (lectoparatypes, *L. latifrontale*, Boulenger, 1894a, 1894b). Col. Elisa: N.R.M. Nos. 2897A, 2897B. Apa-Bergland: Z.S.M. No. 231/1933. Luque: I.M.Z.U.T. No. 972 (holotype *L. camerani*, Peracca, 1895a). Primavera: B.M. Nos. 1955.1.5.85, 1956.1.3.27–1956.1.3.30, 1956.1.16.27, 1958.1.2.10, 1958.1.2.11, 1960.1.2.92, 1960.1.2.93, 1962.27; C.G. Nos. 1595, 1596. Colonia Nueva Italia: F.M.N.H. No. 42290; M.C.Z. No. 47030.

BIOLOGY: Gans, Huang, and Clark (1967; also Huang, Clark, and Gans, 1967) described the chromosome numbers of this species as $2N = 32-34$, including six pairs of macrochromosomes and 10–11 pairs of microchromosomes. Rosenberg (1967) described the hemipenes and Gans (1969) provided a colored photograph.

A description of the general anatomy, including comments on the eyes, tongue, lungs, the skull, vertebrae, and ribs was furnished by

Müller (1832), whereas Duvernoy (1833) dealt with the intestinal canal. A description of the skull (1944) and the vertebral column (1945) was published by Zangerl.

Schinz (1833) remarked that the species was subterranean, rarely reached the surface, and was considered poisonous because of its "fangs." D'Orbigny (1847) noted that *L. phocaena* occurred in most sandy areas and also in the earthen walls of homes. He also noted that it remained hidden during the day, perhaps under rocks and logs, but emerged at night to search for insects. As it is often found in cemeteries, people believe that it feeds on corpses. The Guaranis call it Ibiyau or dirt eater. Duméril [1855 (1854–1855)] reported that a specimen lived for two-and-one-half months in the Paris menagerie, but I have kept specimens for more than two years.

Goeldi (1897) provided the most detailed report of their biology. He found the species common in the vicinity of Rio de Janeiro and commented on the superstitious dislike of them by local gardeners who encountered superficial tunnels of the species particularly after rains. Goeldi kept them in captivity, feeding them on earthworms. There is reference to the widespread popular view that they live commensal with ants, particularly the leaf cutter (*sauva*) and are hence referred to as "mae de sauva." He also noted that this story appears to represent a widespread animal fable of Indian origin as indicated by its antiquity and wide distribution (cf. Gans, 1962 for similar reports on *Amphisbaena alba*). He described a single clutch (no number given) of eggs taken in March from a pile of bricks and tiles inhabited by *Camponotus* ants. The eggs were soft-shelled, contained well-developed young and measured about 54×19 mm.

The museum collections examined for the present study provided various poorly preserved series of embryos that seem to pertain to this species. Unfortunately, most of them contain minimum ancillary information. Nevertheless, these specimens are tabulated herein and illustrated (figs. 53 and 54), as some of them, from external evidence, seem to represent much earlier stages than have previously been reported for any amphisbaenian species.

The first sample of three eggs, in very poor condition (M.A.C.N. No. 1055), was taken at Zelaya in Buenos Aires Province, Argentina. A

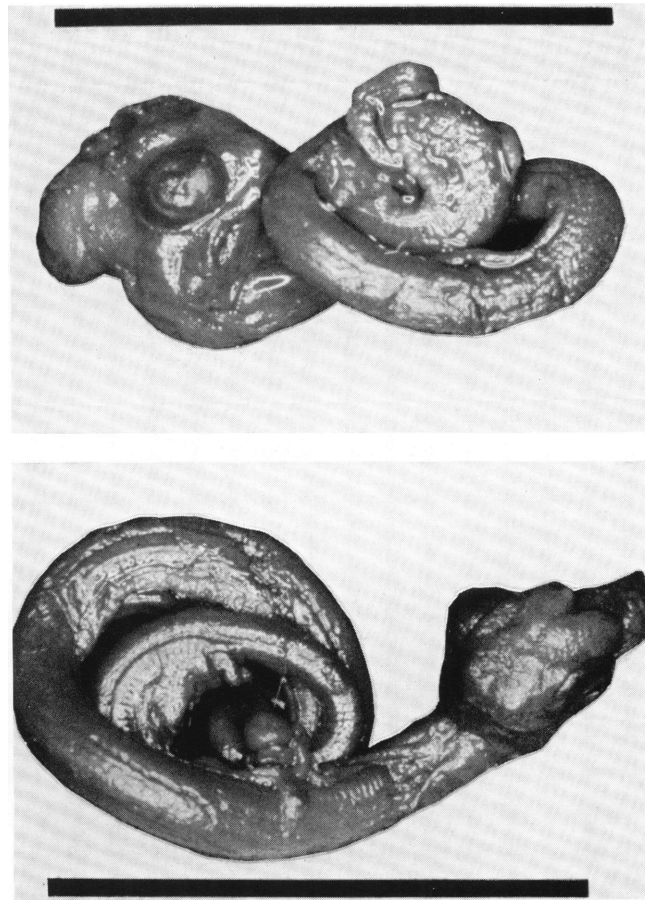


FIG. 53. *Leposternon microcephalum*(?). Photographs of two early embryos collected by Wilhelm Ehrhardt in the region of the Itapocú, Humboldt District, Santa Catarina, Brazil, on December 17, 1907. Black line equals 1 cm. to scale.

second sample (B.M. Nos. 93.9.30.2, 93.9.30.3) of two fairly large eggs (measuring 52×12 mm. and 45×14 mm. in reconstruction of the apparently partly developed and then shrunken individuals) were taken at Theresópolis, Rio de Janeiro, Brazil. It is uncertain whether these do indeed belong to the species *microcephalum*.

The next two sets of eggs were collected by Wilhelm Ehrhardt within the region of the Itapocú River course, Humboldt District, Santa Catarina, Brazil on December 17, 1907 and the spring of 1908 respectively. Both of these series were collected in anthills. The first (H.M. No. 3572) consists of eight embryos at an early stage (eyes prominent, protruding hemispheres of brain forming most notable aspect of head, body coiled in regular helix, caudal region much less

developed than head, coil diameter from 5 to 7 mm.); some eggshells but no yolk material are preserved in the vial with the specimens. A second series (H.M. No. 3571), taken by the same collector at the same site, consists of two much larger specimens (39 mm. total length, with the cephalic segmentation better developed except on the middorsal line). Here too, the posterior body is coiled but the disproportionate increase in size of the head (fig. 53) gives it an unbalanced appearance.

Four specimens respectively in the Berlin (Z.M.U. No. 32010) and London (B.M. Nos. 1928.11.5.130, 1928.11.5.131) museums and all collected by Wilhelm Ehrhardt at Hansa, Santa Catarina may well have derived from a single clutch. Bits and pieces of eggshell do not permit



FIG. 54. *Leposternon microcephalum*. Top, lateral view of unfolded embryo. Bottom, left, ventral view of folded embryo. Both Z.M.U. No. 32010, collected by Wilhelm Ehrhardt at Hansa, Santa Catarina, Brazil. Bottom, right, dorsal view of embryo, B.M. No. 1928.11.5.130, collected by Wilhelm Ehrhardt at Hansa, Santa Catarina, Brazil. Note prominent eye, gradual formation of head shape and hypertrophy of anterior as opposed to posterior bodily proportions. Thin lines equal 1 cm. to scale.

reconstruction but the embryos all measure approximately 47 mm. in length. Rather than being spirally coiled, the body now lies in an oval coil consisting of three straight stretches and a circularly curled terminal portion. The head is still at least twice the diameter of the tail but the dermal segmentation is well expressed at this stage.

The largest specimens are a series of four

(A.Z.M. No. 10177) collected by Goeldi at Theresópolis, Rio de Janeiro, Brazil, and apparently contained in eggshells, one of which (carefully stuffed with cotton) appears to have been 47×14 mm. in proportion. The embryos are approximately 64 mm. long but still folded into three and a half loops as were the previous ones.

Schreitmüller (1926) kept specimens in a

terrarium and noted that they fed on mealworms, earthworms, and centipedes, as well as many types of subterranean insects. His specimens showed a shriveled, folded skin when kept in dry soils.

Engmann (1927) supplemented Schreitmüller's report with field observations made during January in Rio de Janeiro including a photo of a clutch of two eggs (57 and 54 mm. length, 16.8 and 16 mm. mid-diameter, 11 (9.5) and 9.5 mm. diameter at each end) and placed in an oval, 80 by 45 mm. smooth walled cavity found 23 to 25 cm. below the surface of a truck garden. He commented on the smoothness of the inside wall of the cavity and its non-absorption of free water. Rather than accept the (clearly appropriate) view that the species used its head to compact the walls (cf. Kaiser, 1955), he as-

sumed that the *Leposternon* waterproofed it by means of a secretion.

Specimens kept in my laboratory for more than two years attacked any small insects or worms (fig. 55) and definitely required moist soil (cf. Gans, 1968). Herndon G. Dowling kindly informed me that a specimen in the Bronx Zoo bit chunks from pieces of smelt left on the surface of the soil.

***Leposternon octostegum* (Duméril)**

Lepidosternon octostegum DUMÉRIL, 1851, p. 149. *Terrapin* *typica*: "Brésil." Holotype: M.H.N.P. No. 7055.

Lepidosternon otostegum DUMÉRIL AND BOCOURT, 1882, p. 494. (*Lapsus* hence not available; Stoll and others, 1961, art. 33b.)

DISTRIBUTION RECORDS: BRAZIL:—M.H.N.P. No. 7055 (holotype; Duméril, 1851; Peters, 1879, fig. 1; Strauch, 1881). Bahia: (Strauch, 1881).

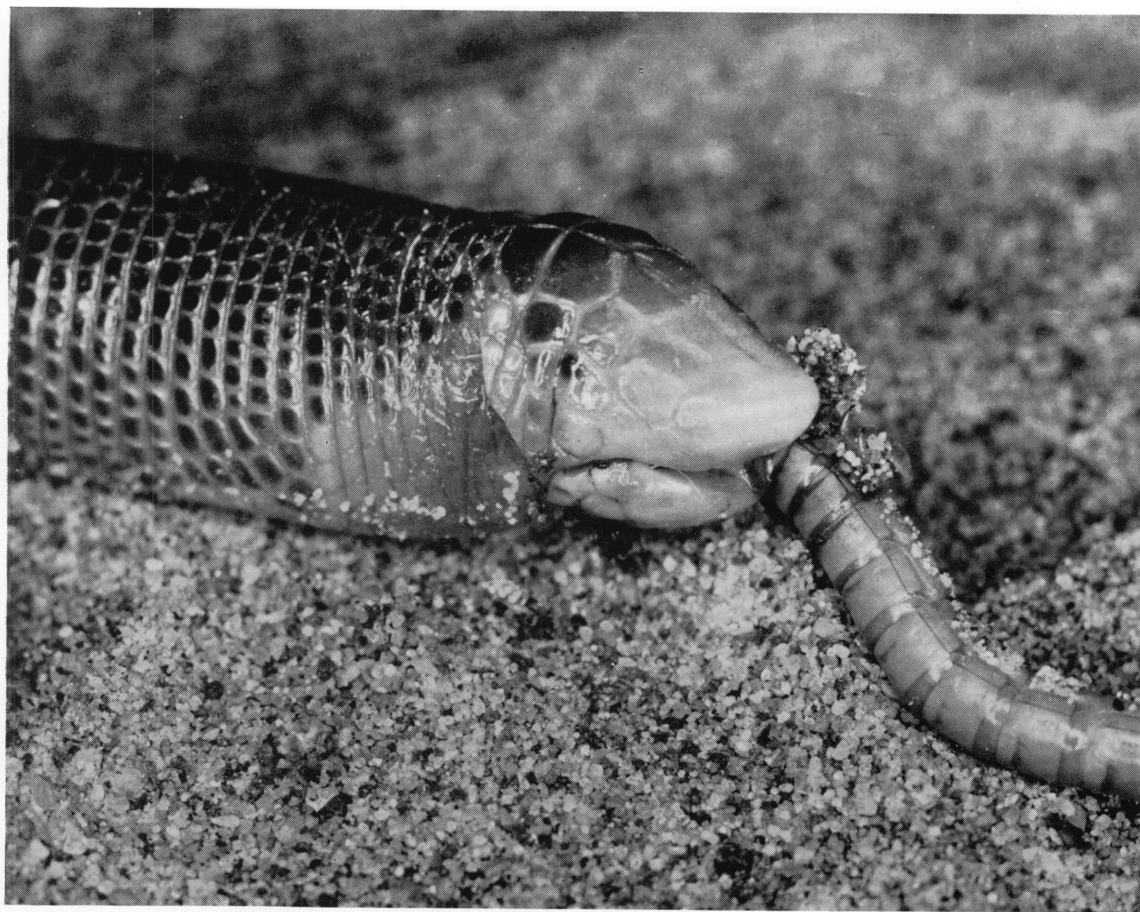


FIG. 55. *Leposternon microcephalum*. Captive specimen feeding on mealworm (*Tenebrio*) larva.

Leposternon polystegum (Duméril)

Lepidosternon polystegum DUMÉRIL, 1851, p. 149. *Terra typica*: "Bahia," Brazil. Holotype: M.H.N.P. No. 3124.

Lepidosternon grayii GRAY, 1865, p. 452. Name attributed to A. Smith MS. *Terra typica*: "South America." Holotype: B.M. No. 48.6.26.11:RR1946.9.1.7.

Leposternon polystegoides SCHMIDT, 1936, p. 31. *Terra typica*: "Lake Papary, Rio Grande do Norte," Brazil. Holotype: C.A.S. No. 49866. Paratypes: C.A.S. Nos. 49375, 49533, 49534, 49863; F.M.N.H. Nos. 64425, 64426.

DISTRIBUTION RECORDS: BRAZIL:—(Boulenger, 1885a, 1885b); B.M. Nos. 1903.6.29.31, 48.6.26.11:RR1946.9.1.7 (holotype *L. grayii*; Gray, 1865, 1872, 1873; Strauch, 1881; Boulenger, 1885b); M.C.Z. No. 3359; M.G. No. 1010.79; N.H.M.G. No. 91; Z.M.U. Nos. 1397A, 1397B (Peters, 1879, fig. 3; Strauch, 1881). (Argentina, mouth of the Rio Negro): N.M.W. No. 17. *Pará*:—M.P.E.G. Nos. 198, 199; N.H.M.B. No. 68D. *Tajapurú*: M.C.Z. No. 4659. *Rio Grande do Norte*: Lake Papari (now Nisia Floresta): C.A.S. No. 49866 (holotype *L. polystegoides*, Schmidt, 1936; Schmidt and Inger, 1951; Slevin and Leviton, 1956), F.M.N.H. Nos. 64425, 64426 (paratypes *L. polystegoides*, Schmidt, 1936; Schmidt and Inger, 1951; Marx, 1958). *Pernambuco*:—B.M. Nos. 87.12.2.3, 87.12.2.4 (Sclater, 1880; Strauch, 1881; Boulenger, 1885b); U.S.N.M. Nos. 58347, 58348 (Burt and Burt, 1930); Z.M.U. No. 9808. *Recife*: B.M. No. 81.1.17.11. *Bahia*:—M.H.N.P. No. 3124 (holotype *L. polystegum*; Duméril, 1851; Strauch, 1881). *Barreiras*: U.M.M.Z. No. 103078.

BIOLOGY: Boulenger (1885a) demonstrated a specimen that had been half swallowed by a coral snake and emerged from the side of the snake. Although the preparation is still preserved in the collection of the British Museum, it is not quite clear whether this was a real event.

Leposternon scutigera (Hemprich)

Amphisbaena scutigera W. HEMPRICH, 1820, p. 117. *Nomen nudum* as published without description.

Amphisbaena scutigera F. G. HEMPRICH, 1829, p. 129. *Terra typica*: "Brasília." Holotype: Z.M.U. No. 1398.

Lepidosternon hemprichii WIEGMANN AND RUTHE, 1831, p. 186. New name for *Amphisbaena scutigera* Hemprich; redescription in Wiegmann (1834, p. 20) and in Wiegmann (1836, p. 153) where considered distinct species.

Cephalopeltis cuvieri J. MÜLLER, 1832, p. 256. *Terra typica*: "Brésil." Lectotype: M.H.N.P. No. 3125 by present designation.

Lepidosternon scutigerum DUMÉRIL and BIBRON, 1839, p. 509. Emendation.

DISTRIBUTION RECORDS: No Locality: H.M. No. 1684; M.G. No. 1010.78; N.M.B. No. 3817 (F. Müller, 1878; Strauch, 1881); P.U.M. Nos. 119A, 119B.

BRAZIL:—A.N.S.P. No. 9681; B.M. Nos. 68.9.16.24 (Boulenger, 1885a), 94.6.29.28 (Christiana Museum), 1904.2.2.2; C.A.S. No. 86647; I.M.Z.U.T. No. 326; K.M. No. R4491; M.H.N.P. Nos. 3125, 3126 (see footnote on p. 405), 3127, 5285; M.L.U. Nos. 4A, 5, 6; N.H.M.B. Nos. 70A₁, 70A₂, 70B; N.M.W. No. 12375 (?Fitzinger, 1860); P.U.M. No. 118; Z.I.L. Nos. 317–319, 320 (Strauch, 1881), 3314; Z.M.U. Nos. 1398 (holotype *A. scutigera* F. G. Hemprich, [also W. Hemprich, 1820], 1829; Wiegmann, 1836; Lichtenstein, 1856; Strauch, 1881), 1399, 7666; Z.S.M. No. 475/1920. *Rio de Janeiro*: Caxias: U.S.N.M. No. 5670 (Girard, 1858; Burt and Burt, 1930). *Rio de Janeiro*: N.M.W. Nos. 12376:1, 12376:2; (Girard, 1858; Boulenger, 1885b). *Icarahy*, *Niterói*: B.M. No. 1924.9.20.15.

BIOLOGY: Miscellaneous comments on the anatomy of this species are found in Müller (1832). Duméril [1854–1855 (1855)] noted that a specimen lived for 11 months in captivity.

Leposternon wuchereri (W. C. H. Peters)

Lepidosternon wuchereri W. C. H. PETERS, 1879, p. 276. *Terra typica*: "Bahia," Brazil. Holotype: Z.M.U. No. 9389.

Lepidosternum sinuosum PERACCA, 1895b, p. 1. *Terra typica*: "Brasile." Holotype: I.M.Z.U.T. No. 1108.

DISTRIBUTION RECORDS: BRAZIL:—I.M.Z.U.T. No. 1108 (holotype, *L. sinuosum*, Peracca, 1895b). *Bahia*: ?Porto Seguro: N.M.W. No. 12373. *Andaraí*: Z.M.U. No. 9389 (holotype, *L. wuchereri*, Peters, 1879, fig. 2). *Espírito Santo*: Linhares (Refugio Sooretama): C.G. No. 3721. *Rio de Janeiro*:—N.M.W. No. 12372 (Steindachner, 1867; Strauch, 1881).

Leposternon species

Here I refer to M.P.E.G. No. 1185, a single specimen from Aragarças, Goiás, Brasil. The discussion (under Recognition of Species in Space, *L. infraorbitale*) and illustrations (figs. 9, 21, 23, 24, 50–52) document my reasons for considering it distinct.

INCERTAE SEDIS

DISTRIBUTION RECORDS: BRAZIL:—(Gray, 1873; Barbier, 1904; Themido, 1945). *Rio Branco*: D.Z. *Goiás*: Santa Isabel, Ilha do Bananal: D.Z. *Pedro Alfonso*: D.Z. *Pará*: Belem: D.Z. *Maranhão*: Barra do Corda: D.Z. *Piauí*: Piripiri: D.Z. *Ceará*:—D.Z.

Fernando de Noronha:—D.Z. *Pernambuco*: Recife: D.Z. *Bahia*: Villa Nova (=Senhor de Bonfim): D.Z. *Espirito Santo*: Rio Doce: D.Z. Chavez: D.Z. Porto Cachoeiro: D.Z. *Minas Gerais*: Rio Pandeiro: D.Z. (Amaral, 1935). Sereno: D.Z. Uberlândia: D.Z. Vargem Alegre: D.Z. Viçosa: D.Z. *Rio de Janeiro*: Teresópolis: D.Z. (Müller, 1927). Caxias: D.Z. Rio de Janeiro, Gb.: D.Z. (Hensel, 1868; Goeldi, 1902). Manguinhos, Gb.: D.Z. Guanabara, Gb.: D.Z. Angra dos Reis: D.Z. Mendez: D.Z. Ilha Grande: D.Z. *Sao Paulo*: Sao Paulo: D.Z. Bom Jardim: D.Z. Queimada Grande Isl.: D.Z. (Hoge, 1950). Piquette: D.Z. Santos: D.Z. Cachoeira: D.Z. Franca: D.Z. Bauru: D.Z. Java: D.Z. Itapeverica da Serra: D.Z. Santo Anastacio: D.Z. Ribeirão Pires: D.Z. Registro: D.Z. Lins: D.Z. Peruibe: D.Z. Ilha de São Sebastião: D.Z. Ouro Branco: D.Z. Cubatão: D.Z. Ubatuba: D.Z. Ilha dos Alcatrazes: D.Z. São Vicente, near Santos: D.Z. Itanhaen: D.Z. Barueri: D.Z. Santo Amaro: D.Z. Piracicaba: D.Z. Rubial Tr.: D.Z. Bertioga: D.Z. Candido Mota: D.Z. Avahandava: D.Z. Jardinopolis: D.Z. Aguapé: D.Z. Alegrim (=Pedro de Toledo), near Peruibe: D.Z. Guararapes: D.Z. Camborene: D.Z. Itaraguatutuba: D.Z. São Vicente (near Santos): D.Z. *Parana*: Paranaguá: D.Z. Antonina: D.Z. *Santa Catarina*:—D.Z. (Lampe, 1911). Hansa: D.Z.

ARGENTINA: *Buenos Aires*:—D.Z. (Gray, 1865). *Corrientes*:—D.Z. (Koslowsky, 1898). *Entre Rios*:—

D.Z. (Koslowsky, 1898). *Gran Chaco*:—D.Z. (Koslowsky, 1898).

BIOLOGY: The majority of records could not be assigned to a particular species and are hence summarized below for the genus.

The skull has been variously illustrated and discussed by Gervais (1853), and particularly by Jollie (1960). Palatal details were given by Lakjer (1927) and the head muscle arrangements were illustrated by Lakjer (1926). General and miscellaneous statements on their anatomy are presented in Gervais (1853), Stannius (1856), Carus and Gerstaecker (1868), Cope (1892, 1900), and Camp (1923). The occurrence, arrangement, and muscles of the pectoral elements are variously documented in Rathke (1853), Parker (1868), and Fürbringer (1870, 1900). Wiedemann (1932) illustrated some of the superficial locomotor muscles. The arterial system was reported on by Rathke (1857, 1863) and Hochstetter (1898), the lungs by Milani (1894) and Butler (1895), and the intestines by Jacobshagen (1920, 1937), and Pernkopf and Lehner (1937).

Wiedemann (1932) and also Kaiser (1955) commented on the locomotor pattern.

SUGGESTIONS FOR FUTURE WORKERS

THE PRESENT PAPER and one dealing with the monotypic genera, *Bronia*, *Aulura*, and *Mesobaena* mark the final step in a first-stage review of South American amphisbaenians. A few individual samples remain to be described in the genus *Amphisbaena*, particularly the species *plumbea* of Gray, *polygrammica* of Werner, and *gracilis* of Strauch. At the same time, I hope now to proceed to an analysis of higher categories within the Amphisbaenia and to utilize some of the morphological, karyological, and behavioral information already accumulated. The series of studies of which the present paper forms a part will next deal with a detailed analysis of more functional aspects, among which the work of locomotor and feeding patterns is already well-advanced (cf. Gans, 1968, 1969).

These studies, however, are intended to stimulate work by others as well as to serve as a basis for further analysis by me. For these reasons, it may be useful to point out some considerations that would benefit from attention:

1. All the taxonomic schemes here presented need tests on the basis of additional specimens with more accurate locality data. The ranges of the various species need to be defined, particularly in view of the fact that most of these are here estimated upon very old museum specimens with inadequate locality data.

2. The relationships of the various species require characterization. For this purpose are needed both a better comprehension of their structural pattern and information about characteristics more recently utilized in taxonomy, namely, their chromosome configuration and the chemistry of their blood and plasma. I am prepared to look into such matters; on the other hand, it seems more appropriate that a study of this kind be carried out in Brazil where most of the species occur and living specimens are most likely to be available.

3. I lack significant ecological information about the areas occupied by these animals in zones where they occur both allopatrically or sympatrically. Vanzolini (1968) has suggested

some relation between the character pattern and temperature for a most limited sample of *Amphisbaena alba*, but Osgood's (1968) experiments do not show a definite correlation between temperature and any meristic character. It will be interesting to see whether the suggested pattern holds up as additional materials become available; and whether a similar correlation also occurs in other species.

It is obvious that ecological analysis must be coupled with a taxonomically oriented study in order to indicate the basis for ecological replacement. More important, such analysis may ultimately permit one not only to establish reasons why situations of sympatry are possible, but also to assist in understanding situations of extreme variability such as that found in Paraguay.

SUMMARY

The present study, based on more than 800 specimens in some 40 collections and on a review of all references in the literature, reduces the more than 24 named forms of the South American amphisbaenian genus *Leposternon* to seven, six of these having been previously named, and the seventh thus far known from only a single specimen. The species *Leposternon microcephalum* occupies almost the entire generic range, whereas the remaining forms (*L. infraorbitale*, *L. octostegum*, *L. polystegum*, *L. scutigerum*, *L. wuchereri*) appear to be more or less sympatric to it. The single, yet unnamed individual of the seventh form stems from Goiás, within the range of *L. infraorbitale*.

The variability of integumentary architecture is much greater in this genus than in those other amphisbaenians thus far examined. The cephalic segmentation of some of the species in particular shows remarkable local variance, and the dermal-vertebral ratio is most irregular, departing drastically from the value of two, which is almost universal in other species of the order; some local variants particularly would seem to provide raw material for several kinds of interesting supplementary studies.

LITERATURE CITED

- AGASSIZ, JEAN LOUIS RODOLPHE
1833-1843. Recherches sur les poissons fossiles.
Neuchâtel, Petitpierre, vol. 4, pp. 1-269.
1848. Nomenclator zoologici. Index universalis,
continens nomina systematica classium.
Solothurn, x+1135 pp.

- ALEXANDER, A. ALLAN, AND CARL GANS
1966. The pattern of dermal-vertebral correlation in snakes and amphisbaenians. *Zool. Meddel.*, Leiden, vol. 41, no. 11, pp. 171-190.
- AMARAL, AFRANIO DO
1935. *Collecta herpetologica no Centro do Brasil*. Mem. Inst. Butantan, vol. 9, pp. 235-246.
- BARBIER, H.
1904. Les reptiles du Musée d'Elbeuf. *Amphisbénien et ophiidiens*. Bull. Soc. Etude Sci. Nat. Mus. Hist. Nat. Elbeuf, vol. 22, pp. 41-63.
- BERTHOLD, ARNOLD ADOLPH
1859. Einige neue Reptilien des akad. zoolog. Museums in Göttingen. *Nachr. G. A. Univ. K. Gesell. Wiss. Göttingen*, vol. 17, pp. 179-181.
- BLYTH, EDWARD
1853. Notices and descriptions of various reptiles, new or little known. *Jour. Asiatic Soc. Bengal*, vol. 22, pp. 639-655.
- BOETTGER, OSKAR
1885. Liste von Reptilien und Batrachiern 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.
- BOND, JAMES, AND RODOLPH M. DE SCHAUENSEE
1942. The birds of Bolivia. Part 1. *Proc. Acad. Nat. Sci. Philadelphia*, vol. 94, pp. 307-391.
- BOULENGER, GEORGE ALBERT
1885a. Exhibition of, and remarks upon, specimens of an amphisbaenoid lizard and coral-snake from Brazil. *Proc. Zool. Soc. London*, pt. 2, pp. 327-328.
1885b. Catalogue of the lizards in the British Museum (Natural History). Second edition. London, vol. 2, xiii+497 pp.
1890. First report on additions to the lizard collection in the British Museum (Natural History). *Proc. Zool. Soc. London*, pp. 77-86.
1894a. List of reptiles and batrachians collected by Dr. T. Bohls near Asuncion, Paraguay. *Ann. Mag. Nat. Hist.*, ser. 6, vol. 13, pp. 342-348.
1894b. Second report on additions to the lizard collection in the Natural History Museum. *Proc. Zool. Soc. London*, pp. 722-736.
- BRONGERSMA, L. D.
1932. Abnorme Beschilderung des Kopfes bei Amphisbaenen. *Zool. Anz.*, vol. 99, nos. 5-6, pp. 132-134.
- 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, no. 6, pp. 1-52.
1931. South American lizards in the collection of the American Museum of Natural History. *Bull. Amer. Mus. Nat. Hist.*, vol. 61, art. 7, pp. 227-395.
- BUTLER, GERARD W.
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. *Proc. Zool. Soc. London*, pp. 691-712.
- CAMP, CHARLES L.
1923. Classification of the lizards. *Bull. Amer. Mus. Nat. Hist.*, vol. 48, art. 11, pp. 289-481.
- CARUS, JULIUS VICTOR, AND C. E. A. GERSTAECKER
1868. Reptilia. In *Handbuch der Zoologie*. Leipzig, Wilhelm Engelmann, vol. 1, pp. 368-432.
- COPE, EDWARD DRINKER
1887. Synopsis of the batrachia and reptilia obtained by H. H. Smith, in the Province of Mato Grosso, Brazil. *Proc. Amer. Phil. Soc.*, vol. 24, no. 125, pp. 44-60.
1892. The osteology of Lacertilia. *Proc. Amer. Phil. Soc.*, vol. 30, no. 138, pp. 185-221.
1900. The crocodilians, lizards and snakes of North America. *Rept. U.S. Natl. Mus. for 1898*, pp. 153-1294.
- DEVINCENZI, GARIBALDI J.
1925. Fauna erpetológica del Uruguay. *An. Mus. Hist. Nat. Montevideo*, ser. 2, vol. 2, pp. 1-65.
- D'ORBIGNY, ALCIDE D.
1847. Reptiles. In *Voyage dans l'Amérique Méridionale*. Paris and Strassburg, Bertrand and Levrault, vol. 5, pt. 1, 12 pp.
- DUMÉRIL, ANDRÉ MARIE CONSTANT, AND GABRIEL BIBRON
1839. *Erpétologie générale ou histoire naturelle complète des reptiles*. Paris, vol. 5, 855 pp.
- DUMÉRIL, AUGUSTE HENRY ANDRÉ (not Duméril, André Marie Constant, and August Henri André Duméril)
1851. Catalogue méthodique de la collection des reptiles du Muséum d'Histoire Naturelle de Paris. Paris, iv+224 pp.
- DUMÉRIL, AUGUSTE HENRY ANDRÉ
1854-1855. Notice historique sur la ménagerie des reptiles. *Arch. Mus. Natl. d'Hist. Nat.*, Paris, vol. 7, pp. 193-320.
1856. Note sur les reptiles du Gabon. *Rev. Mag. Zool. pure et appliquée... Guéron-Méneville*, ser. 2, vol. 8, pp. 417-424.
- DUMÉRIL, AUGUSTE HENRY ANDRÉ, AND FERNAND BOCOURT
1882. Mission scientifique au Mexique et dans l'Amérique centrale. Troisième partie.

- Études sur les reptiles et les batraciens. Paris, sect. 8, pp. 493-494.
- DUVERNOY, GEORGES LOUIS
1833. Fragmens d'anatomie sur l'organisation des serpens. Ann. Sci. Nat., vol. 30, pp. 1-79.
1839-1842. Reptiles. In Cuvier, Georges, Le Règne Animal. . . . Paris, Fortin, Masson et Cie, 169 pp.
- ENGMANN, P.
1927. Beitrag zur Biologie von *Lepidosternon microcephalum* Wglr. Lacerta, Zeitschr. Vivarienkunde, no. 11, pp. 45-46.
- FITZINGER, LEOPOLD J.
1826. Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften. Vienna, vi+66 pp.
1843. Systema reptilium. Fasciculus primus Amblyglossae. Vienna, Braumüller and Seidel, 106+viii pp.
1860. Die Ausbeute der österreichischen Naturforscher an Säugethieren und Reptilien während der Weltumsegelung Sr. Majestät Fregatte Novara. Sitzber. K. Acad. Wiss., Math.-Naturwiss. Cl. Vienna, vol. 42, no. 25, pp. 383-416.
- FÜRBRINGER, MAX
1870. Die Knochen und Muskeln der Extremitäten bei den schlangenähnlichen Saurien. Vergleichend - anatomische - Abhandlung. Leipzig, W. Engelmann, vi+136 pp.
1900. Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln. Jena. Zeitschr. Naturwiss., vol. 34, pp. 215-718.
- GANS, CARL
1962. Notes on amphisbaenids (Amphisbaenia: Reptilia). 5. A redefinition and a bibliography of *Amphisbaena alba* Linné. Amer. Mus. Novitates, no. 2105, pp. 1-31.
1966. Studies on amphisbaenids (Amphisbaenia, Reptilia). 3. The small species from southern South America commonly identified as *Amphisbaena darwini*. Bull. Amer. Mus. Nat. Hist., vol. 134, art. 3, pp. 185-260.
1967. A check list of recent amphisbaenians (Amphisbaenia, Reptilia). *Ibid.*, vol. 135, art. 2, pp. 61-106.
1968. Relative success of divergent pathways in amphisbaenian specialization. Amer. Nat., vol. 102, no. 926, pp. 345-362.
1969. Amphisbaenians—reptiles specialized for a burrowing existence. Endeavour, vol. 28, no. 105, pp. 146-151.
[In press]. Comments on the types and some other interesting amphisbaenians in the collection of the Zoological Institute at Leningrad. Zool. Zhour.
- 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 H. FRED CLARK
1967. The diphyletism of the Amphisbaenia (Reptilia). A reevaluation based upon chromosome counts. Copeia, no. 2, pp. 485-487.
- GERVAIS, PAUL
1853. Recherches sur l'ostéologie de plusieurs espèces d'amphibènes, et remarques sur la classification de ces reptiles. Ann. Sci. Nat. Paris, ser. 3, vol. 20, pp. 293-312.
- GIRARD, CHARLES FREDERICK
1858. Herpetology. United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N., vol. 20, private reprint by J. B. Lippincott and Co., Philadelphia, xvii+496 pp. (The official version reads "Prepared under the superintendence of S. F. Baird.")
- GOELDI, EMIL A.
1897. Die Eier von 13 brasilianischen Reptilien, nebst Bemerkungen über Lebens- und Fortpflanzungsweise letzterer. Beobachtungen aus den Jahren 1884-1897. Zool. Jahrb., Abt. Syst. Geogr. Biol. Thiere, vol. 10, no. 5, pp. 640-676.
1902. Lacertilios. Lagartos do Brazil. Bol. Mus. Paraense, vol. 3, nos. 3-4, pp. 499-560.
- GRAY, JOHN EDWARD
1825. A synopsis of the genera of reptiles and amphibia, with a description of some new species. Thomson Ann. Phil., ser. 2, vol. 10, pp. 193-217.
1844. Catalogue of the tortoises, crocodiles, and amphisbaenians in the collection of the British Museum. London, viii+80 pp.
1865. A revision of the genera and species of amphisbaenians with the descriptions of some new species now in the collection of the British Museum. Proc. Zool. Soc. London, pp. 442-455.
1872. Catalogue of shield reptiles in the collection of the British Museum. Part II. Emydosaurians, rhynchocephalian, and amphisbaenians. London, vi+41 pp.
1873. Handlist of the specimens of shield reptiles in the British Museum. London, iv+124 pp.
- GRIFFIN, LAWRENCE EDMONDS
1917. A list of the South American lizards of the Carnegie Museum, with descriptions of four new species. Ann. Carnegie Mus., vol. 11, nos. 1-2, pp. 302-320.

- GRIFFITH, EDWARD, AND EDWARD PIDGEON
1831. The class reptiles arranged by the Baron Cuvier, with specific descriptions. London, Whittaker, Treacher and Co., 481 pp.
- GUICHENOT, ALPHONSE
1855. Reptiles. In Castelnau, Francis de, Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro à Lima, et de Lima au Para; . . . Paris, 96 pp.
- HANSON, EARL PARKER
1945. Index to map of Hispanic America 1:1,000,000. American Geographical Soc. Publ. No. 5, U.S. Government Printing Office, Washington, D.C., 923 pp.
- HELLMICH, WALTER
1960. Die Sauria des Gran Chaco und seiner Randgebiete. Bayerischen Akad. Wiss. Math. Nat. Kl., new ser., no. 101, 131 pp.
- HEMPRICH, F. G.
1829. Amphisbaenarum generis novas species duas descripsit. Verhandl. Gesell. Naturf. Fr., Berlin, vol. 1, no. 2, pp. 129-130.
- HEMPRICH, WILHELM
1820. Grundrisse der Naturgeschichte für höhere Lehranstalten. Berlin and Vienna, Aug. Rücker, pp. 114-125.
- HENSEL, REINHOLD
1868. Beiträge zur Kenntniss der Wirbelthiere Südbrasilens. Arch. Naturgesch., vol. 34, no. 1, pp. 323-375.
- HOCHSTETTER, F.
1898. Über die Arterien des Darmkanals der Saurier. Morph. Jahrb., vol. 26, no. 2, pp. 213-273.
- HOFFSTETTER, ROBERT, AND JEAN-PIERRE GASC
1969. Vertebrae and ribs in modern reptiles. In Gans, C., A. d'A. Bellairs, and T. S. Parsons, eds., Biology of the Reptilia. London, Academic Press, vol. 1, chapter 5, pp. 201-310.
- HOGUE, ALPHONSE RICHARD
1950. Notas erpetológicas. 7. Fauna erpetológica da Ilha da Queimada Grande. Mem. Inst. Butantan, vol. 22, pp. 151-172.
- HUANG, CHESTER, H. FRED CLARK, AND CARL GANS
1967. Karyological studies on fifteen forms of amphisbaenians (Amphisbaenia: Reptilia). Chromosoma (Berlin), vol. 22, no. 1, pp. 1-15.
- IHERING, HERMANN VON
1898. Contributions to the herpetology of São Paulo, Brazil. I. Proc. Acad. Nat. Sci. Philadelphia, pp. 101-109.
- JACOBSHAGEN, E.
1920. Zur Morphologie des Oberflächenreliefs der Rumpfdarmschleimhaut der Reptilien. Jena Zeitschr., vol. 56, pp. 361-430.
1937. IV. Mittel- und Enddarm (Rumpfdarm). In Bolk, Louis, Ernst Göppert, Erich Kalilius, and Wilhelm Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Berlin and Vienna, vol. 3, pp. 563-724.
- JOLLIE, MALCOLM T.
1960. The head skeleton of the lizard. Acta Zool., vol. 41, nos. 1-2, pp. 1-64.
- KAISER, PETER
1955. Über die Fortbewegungsweise der Doppelschleichen. Beobachtungen an *Leposternon microcephalus* (Wagl.). Zool. Anz., vol. 154, pp. 61-69.
- KERFOOT, W. CHARLES
1970. The effect of functional changes upon the variability of lizard and snake body scale numbers. Copeia, no. 2, pp. 252-260.
- KOSLOWSKY, JULIO
1898. Enumeracion sistemática y distribucion geográfica de los reptiles Argentinos. Rev. Mus. La Plata, pt. 1, vol. 8, pp. 161-200.
- LAKJER, TAGE
1926. Studien über die Trigeminus-versorgte Kaumuskulatur der Sauropsiden. Copenhagen, 155 pp.
1927. Studien über die Gaumenregion bei Sauriern im Vergleich mit Anamniern und primitiven Sauropsiden. Zool. Jahrb. Abt. Anat. Ontog. Thiere, vol. 49, pp. 57-356.
- LAMPE, ED.
1911. Erster Nachtrag zum Katalog der Reptilien und Amphibien Sammlung des Naturhistorischen Museums der Stadt Wiesbaden. Jahrb. Nassau Ver. Naturk. Wiesbaden, vol. 64, pp. 137-236.
- LICHTENSTEIN, MARTIN HEINRICH CARL
1856. Nomenclator reptilium et amphibiorum Musei Zoologici Berolinensis. Namenverzeichnis der in der zoologischen Sammlung der königlichen Universität zu Berlin aufgestellten Arten von Reptilien und Amphibien nach ihren Ordnungen, Familien und Gattungen. Berlin, iv+48 pp.
- LIEBERMANN, JOSÉ
1939. Catálogo sistemático y zoogeográfico de los lacertilios argentinos. Physis, vol. 16, pp. 61-82.
- MARX, HYMEN
1958. Catalogue of type specimens of reptiles and amphibians in Chicago Natural History Museum. Fieldiana, vol. 36, no. 4, pp. 409-496.
- MASI, LUIGI
1911. Due nuove specie di *Amphisbaena* della Repubblica argentina. Roma Boll. Soc. Zool. Italiana, ser. 2, vol. 12, nos. 9-12, pp. 229-234.

- MERTENS, ROBERT
1955. Eine brasilianische Inselfahrt. 1. Queimada Grande, die Insel der Giftschlangen. Natur und Volk, vol. 85, no. 10, pp. 305-314.
- MILANI, A.
1894. Beiträge zur Kenntniss der Reptilienlunge. I. Lacertilia. Inaugural-Dissertation zur Erlangung der Doctorwürde der philosophischen Facultät der Grossherzoglichen Ludwigs-Universität zu Giessen. Jena, 47 pp. Also Zool. Jahrb., Abt. Anat. Ontog. Thiere, vol. 7, pp. 545-592.
- MÜLLER, FRITZ
1878. Katalog der im Museum und Universitätskabinet zu Basel aufgestellten Amphibien und Reptilien nebst Anmerkungen. Verhandl. Naturf. Gesell. Basel, vol. 6, pp. 561-709.
1885a. Erster Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. *Ibid.*, vol. 7, pp. 120-165.
1885b. Dritter Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. *Ibid.*, vol. 7, pp. 274-299.
1890. Fünfter Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. *Ibid.*, vol. 8, pp. 249-296.
- MÜLLER, JOHANNES
1832. Beiträge zur Anatomie und Naturgeschichte der Amphibien . . . 8. Zur Anatomie der Genera *Chirotres*, *Lepidosternon*, *Amphisbaena* und einer neuen Gattung aus der Familie der Amphisbaenoidea, *Cephalopeltis*. In Tiedemann, Friedrich, G. R. Treviranus, and L. C. Treviranus, Zeitschrift für Physiologie, Untersuchungen über die Natur des Menschen, der Tiere und der Pflanzen. Heidelberg and Leipzig, vol. 4, no. 2, art. 19, pp. 190-275.
- MÜLLER, LORENZ
1927. Amphibien und Reptilien der Ausbeute Prof. Bresslau's in Brasilien 1913-14. Abhandl. Senckenbergischen Naturf. Gesell., vol. 40, no. 3, pp. 259-304.
- OSGOOD, DAVID WILLIAM
1968. The effects of temperature on the development of meristic characters in the banded water snake. Diss. Ph.D. Duke Univ. x+107 pp.
- PARKER, WILLIAM KITCHEN
1868. A monograph on the structure and development of the shoulder-girdle and sternum in the Vertebrata. London, Ray Society, xii+237 pp.
- PERACCA, MARIO GIACINTO
1895a. 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.
1895b. Nuovà specie di *Lepidosternum* del Museo Zoologico di Torino. *Ibid.*, vol. 10, no. 200, pp. 1-2.
1904. Viaggio del Dr. A. Borelli nel Matto Grosso brasiliano e nel Paraguay, 1899. IX. Rettili ed anfibi. *Ibid.*, vol. 19, no. 460, pp. 1-15.
- PERNKOPF, EDUARD, AND JOSEPH LEHNER
1937. III. Vorderdarm. A. Vergleichende Beschreibung des Vorderdarmes bei den einzelnen Klassen der Kranioten. In Bolk, Louis, Ernst Göppert, Erich Kallius, and Wilhelm Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere. Berlin and Vienna, vol. 3, pp. 349-476.
- PETERS, WILHELM CARL HARTWIG
1879. Über die Amphisbaenen und eine zu denselben gehörige neue Art (*Lepidosternon wuchereri*). Monatsber. Akad. Wiss. Berlin, pp. 273-277.
- RATHKE, MARTIN HEINRICH
1853. Ueber den Bau und die Entwicklung des Brustbeins der Saurier. Königsberg, 26 pp.
1857. Untersuchungen über die Aortenwurzeln und die von ihnen ausgehenden Arterien der Saurier. Denkschr. Akad. Wiss. Wien, Math. Nat. Cl., vol. 13, no. 2, pp. 51-142.
1863. Untersuchungen über die Arterien der Verdauungswerkzeuge der Saurier. Abhandl. Bayerischen Akad. Wiss., Math. Phys. Cl., vol. 9, no. 1, pp. 125-183.
- REINHARDT, JOHANNES, AND CHRISTIAN FREDERIK LÜTKEN
1861. Bidrag til Kundskab om Brasiliens Padder og Krybdyr. Vidensk. Meddel. Naturhist. For. Kjöbenhavn, nos. 10-15, pp. 143-242.
- ROMER, ALFRED SHERWOOD
1957. The osteology of the Reptilia. Chicago, Univ. Chicago Press, xxi+772 pp.
- ROSENBERG, HERBERT I.
1967. Hemipenial morphology of some amphisbaenids (*Amphisbaenia*: Reptilia). *Copeia*, no. 2, pp. 349-361.
- SCHINZ, HEINRICH RUDOLPH
1833. Naturgeschichte und Abbildungen der Reptilien. Nach den neusten Systemen zum gemeinnützigen Gebrauche entworfen und mit Berücksichtigung für den Unterricht der Jugend bearbeitet. Schaffhausen (Das Thierreich), vol. 3, iv+240 pp.
- SCHMIDT, KARL PATTERSON
1936. Notes on Brazilian amphisbaenians. *Herpetologica*, vol. 1, no. 1, pp. 28-32.
- SCHMIDT, KARL PATTERSON, AND ROBERT F. INGER
1951. Amphibians and reptiles of the Hopkins-Branner Expedition to Brazil. *Fieldiana*, zool., vol. 31, no. 42, pp. 439-465.

SCHREITMÜLLER, WILHELM

1926. *Lepidosternum microcephalum* Wagler und *Leimadophis poecilogyra* Daudin (Korallenotter). *Lacerta, Zeitschr. Vivarienkunde*, no. 16, pp. 62–64.

SCLATER, PHILIP LUTLEY

1880. List of additions to the Society's menagerie during the year 1880. Appendix to *Proc. Zool. Soc., London*, vol. 46, pp. 697–720 (713).

SLEVIN, JOSEPH R., AND ALAN E. LEVITON

1956. Holotype specimens of reptiles and amphibians in the collection of the California Academy of Sciences. *Proc. California Acad. Sci.*, ser. 4, vol. 28, no. 14, pp. 529–560.

SMITH, ANDREW

1848. *Monopeltis capensis*. In *Illustrations of the zoology of South Africa*. London, Reptilia, plate 67 (3 pp.). [See Waterhouse, 1880, for exact dates of publication.]

STANNIUS, HERMANN

1856. Die Amphibien. In Siebold, Ph.-F. von, and Hermann Stannius, *Handbuch der Zoologie*. Zweite Auflage. Berlin, Die Wirbeltiere, vol. 2, 270 pp.

STEINDACHNER, FRANZ

1867. Reptilien. In *Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857–1859, unter den Befehlen des Commodore B. von Wüllerstorff-Urbair*. Vienna, Zoologischer Theil, vol. 1, no. 3, 98 pp.

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. *Mémoires de l'Académie des Sciences de Saint-Petersbourg*, vol. 11, pp. 355–479. *Reprinted*: 1881, *Bull. Acad. Imp. Sci. St. Pétersbourg*, vol. 28, col. 45–131.

THEMIDO, ANTÓNIO ARMANDO

1945. Répteis do Brasil. (Catálogo das coleções do Museu Zoológico de Coimbra.) *Mem. Est. Mus. Zool. Univ. Coimbra*, no. 168 pp. 1–15.

VANZOLINI, PAULO EMILIO

1951. A systematic arrangement of the family Amphisbaenidae (Sauria). *Herpetologica*, vol. 7, no. 3, pp. 113–123.
1955. Contribuições ao conhecimento dos lagartos brasileiros da família Amphisbaenidae Gray, 1825. 5. Distribuição geográfica e biometria de *Amphisbaena alba*. *Arq. Mus. Nac. Rio de Janeiro*, vol. 42, pt. 2, pp. 683–705.

1968. Environmental temperature and number of body annuli in *Amphisbaena alba*: Notes on a cline (Sauria, Amphisbaenidae). *Papéis Avulsos de Zool., São Paulo*, vol. 21, pp. 231–241.

WAGLER, JEAN

1824. *Serpentum Brasiliensium species novae, ou histoire naturelle des espèces nouvelles de serpents*. . . Monaco, Jean de Spix, viii + 75 + (1) pp.
1830. *Natürliches System der Amphibien, mit vorangehender Classification der Säugethiere und Vögel*. Munich, 354 pp.

WATERHOUSE, F. H.

1880. On the date of publication of the parts of Sir Andrew Smith's "Illustrations of the zoology of South Africa." *Proc. Zool. Soc. London*, pp. 489–491.

WERNER, FRANZ

1910. Über neue oder seltene Reptilien des Naturhistorischen Museums in Hamburg. ii. Eidechsen. *Hamburg. Jahrb. Wiss. Anst.*, vol. 27 (1909), suppl. no. 2, 1910, pp. 1–46. *Reprinted*: 1910, *Mitteil. Naturhist. Mus. Hamburg*, vol. 27.

WIED, MAXIMILIAN, PRINZ ZU

1825. *Beiträge zur Naturgeschichte von Brasilien*. Weimar, no. 1, xxii + 612 pp.

WIEDEMANN, EDUARD

1932. Zur Ortsbewegung der Schlangen und Schleichen. *Zool. Jahrb., Abt. Allg. Zool. Physiol. Tiere*, vol. 50, no. 4, pp. 557–596.

WIEGMANN, AREND FRIEDRICH AUGUST

1834. *Herpetologia Mexicana, seu descriptio amphiborum novae hispaniae*. . . Pars prima, saurorum species. Berlin, iv + 54 pp.
1836. Ueber die fusslosen Amphisbaenen mit Brustschildern (*Lepidosternon* Wagl.). *Arch. Naturgesch.*, vol. 2, no. 1, pp. 152–158.

WIEGMANN, AREND FRIEDRICH AUGUST, AND JOHANN FRIEDRICH RUTHE

1831. *Handbuch der Zoologie*. Erste Auflage. Berlin, vi + 622 pp.

WITTE, GASTON-FRANÇOIS DE

1930. Liste des reptiles et batraciens récoltés au Brésil par la Mission Massart (1922–23) et description de sept nouvelles espèces. In *Une Mission biologique belge au Brésil*, vol. 2, pp. 1–18.

ZANGERL, RAINER

1944. Contributions to the osteology of the skull of the Amphisbaenidae. *Amer. Midland Nat.* vol. 31, no. 2, pp. 417–454.
1945. Contributions to the osteology of the postcranial skeleton of the Amphisbaenidae. *Amer. Midland Nat.*, vol. 33, no. 3, pp. 764–780.

